Ecology and Diversity of Wild Bees and Wasps in an Urban Landscape

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Abstract

Bees are a diverse group of essential pollinators and useful for studying the impacts of urban environmental change on local biodiversity. A subset of solitary bee species widespread in cities – the cavity-nesters – nest in plant stems and bored holes in wood and readily use human-made nest boxes comprised of these materials or similar ones. Many solitary wasps that predate on abundant and pest arthropod species also use these nest boxes. Nest boxes provide information on diversity, parasitism, and a plethora of other data on cavity-nesting bees and wasps. The main objective was to detect patterns in cavity-nesting bee and wasp diversity using nest boxes and determine the urban factors that impact their populations. A primary goal was to connect urban gardening, land use planning, and policy more directly with bee populations.

Nest boxes were set up at 200 home gardens, community gardens, urban parks, and green roofs and each monitored by a member of a large network of citizen scientists. Nest boxes were set out in April and retrieved in October over three years (2011-2013). From October to March, bee, wasp, and parasite larvae were removed, then reared and identified to species. From over 27,000 records, 84 species of bees, wasps, and parasites were identified from three years including new records for the Toronto region. More native species were recorded than exotic ones, however the most abundant colonizers were exotic [*Megachile rotundata* Fabricius, *Osmia caerulescens* (Linnaeus)] and half of the colonizers were wasps. The type of urban green space surveyed and increasing habitat availability index (HAI), which included high resolution mapping of seven different land use types within 200m of the nest box, were important for increasing colonization. Diversity and abundance in nest boxes and in particularly that of bees was positively influenced by the 'luxury effect', while wasps and parasites responded negatively to increasing human population density. Nest boxes are useful tools for study of populations of cavity-nesting bees and wasps and can become catalysts for conversation regarding bee populations, diversity, and declines.

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Statement of authorship

By submitting this dissertation for partial fulfillment for the degree of doctor of philosophy, I, James Scott MacIvor acknowledge that it is entirely my own work that was conducted while a graduate student under the supervision of Dr. Laurence Packer in the Department of Biology at York University.

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Chapter 1: Introduction

1.1 Bees and wasps in urban landscapes

Pollination is an essential ecosystem service required to sustain flowering plant diversity, including many edible species we cultivate and depend upon (Klein et al. 2007; Ollerton et al. 2011; Garibaldi et al. 2013). Bees are the most important pollinators and unfortunately their diversity and abundance is declining worldwide for - among many reasons - human land use change and subsequent loss of habitat (Winfree et al. 2009; Potts et al. 2010; Cariveau & Winfree, 2015), but also a high susceptibility of fragmented populations to local extinction (Zayed & Packer, 2005). Urbanization also increases isolation between natural areas and generally has a negative impact on bees (Scheupp et al. 2011; Hennig & Ghazoul, 2011; Kennedy et al. 2013; Harrison & Winfree, 2015) and pollination services (Vanbergen et al. 2013). To encourage bee populations, consideration of bee nesting (Cane et al. 2007), and foraging needs (Smith et al. 2006; Williams & Winfree, 2013), and the size and locations of these resources is required (Cane et al. 2006; Matteson & Langelotto, 2010). There is increasing interest by urban citizens to participate in activities that can enhance habitat for pollinators in their gardens and their community (Goddard et al. 2010; Garbuzov & Ratnieks, 2014; Salisbury et al. 2015). Since many solitary wasps play a role in reducing pests (Mackauer & Völkl, 1993) and share similar nesting requirements as bees (Grissell, 2010; Coudrain et al. 2014), urban citizens might also be persuaded to care for them together with bees.

Many wasps are implicated in the regulation of pest and hyper abundant arthropods, such as aphids, phytophagous beetles, and spiders (Krombein, 1967; Fricke, 1993, Buschini et al. 2010). Wasps also respond similarly to landscape variables as solitary bees (Tylianakis et al. 2006; Fabian et al. 2014). These are used to provision their brood and thereby benefit many of the same plant species dependent on bees for pollination (Grissell, 2010). Investigating their

populations, along with those of bees, might elucidate opportunities for the management of natural pest control of aphids and various defoliating caterpillars and beetles (Mackauer & Völkl, 1993; Harris, 1994).

Wild bees, as well as wasps, naturally live in habitats where nesting substrate and foraging resources are patchily distributed (Cane et al. 2001). In terms of nesting substrates, bees and wasps can generally be divided into those nesting below the ground and those nesting above ground in cavities. Some above ground cavity-nesting bee species are more common in urban areas than ground nesting species (Matteson & Langelotto, 2010; Tonietto et al. 2011). Cavity-nesting bees nest in plant stems, holes bored into wood by beetles, and many other 'dark and dry' holes, including those in urban infrastructure such as nail holes (Butler, 1965; Raw, 1972), and cracks in mortar between bricks (Blochtein & Wittman, 1988). In each nesting hole, a reproductive female will construct brood cells in a linear series from the back of the tunnel to the front. She will partition each brood cell using various materials. Depending on the bee or wasp species this could include cut pieces of leaves, tree resins, mud, or pebbles (Krombein, 1967; Cane et al. 2007).

Bees prefer not to travel more than a few hundred metres between nesting and foraging habitat (Zurbuchen et al. 2010); however, longer and more frequent travel by bees through an unrewarding habitat matrix may be necessary (Cane et al. 2006). In cities this could include roads, between buildings, and other paved areas. Cane et al. (2006) identified urban conditions responsible for shaping bee communities and proposed evaluating environmental matrices based on distance between suitable forage and nesting sites.

Urban bee diversity is correlated with differed local and landscape variables (Hostetler & McIntyre, 2001; Hernandez et al. 2009; Cariveau & Winfree, 2015). The ubiquity of small parcels (e.g. <1 ha) of privately owned land results in local habitat heterogeneity (Troy et al. 2007) and within parcel resolution is rarely captured in studies, which describe this habitat to 'residential' or

'green space' (e.g. Kennedy et al. 2013; Steckel et al. 2014). With improved technology and access to software that can resolve land use at smaller scales in complex urban landscapes, opportunities to enhance our understanding of how species respond to urbanization will increase (Rudd et al. 2002; Cane et al. 2006; Zhou et al. 2011).

1.2 Design promoting urban bees and wasps

Bees and wasps have important functional roles in urban environments and generally respond positively to citizen-led action to enhance their populations (Pawelek et al. 2009). To coexist in cities, a degree of acceptance, education, and stewardship is needed on the part of urban citizens. Many of our activities can affect populations of bees and wasps, both positively and negatively (McFredrick & LeBuhn, 2006; MacIvor et al. 2014; MacIvor & Packer, 2015). For example, gardening using native flowering plants, shrubs, and trees can provide foraging resources for bees (Frankie et al. 2009; Pardee & Philpott, 2014). For nesting resources, discovering nesting sites in use and protecting them (e.g. bees or wasps nesting in garden soil, in a brick wall, under an awning) or creating nesting sites (e.g. nest boxes) are first steps towards integrating wild bee and wasp nesting habitat into garden and landscape design.

Study objectives were fourfold: 1) to investigate the ecology and behaviour of cavity nesting bees and wasps, 2) to monitor their populations spatially and temporally in a large city, 3) to investigate which local landscape and socioeconomic factors impact patterns in diversity directly or indirectly, and finally 4) to assess current practices aimed at enhancing cavity-nesting bees for conservation and promotion of ecosystem services. To examine trends in urban bee and wasp populations, data on colonization rates, diversity, and parasites were gathered from 200 independent locations throughout the city of Toronto representing numerous private home gardens, community gardens, city parks, and rooftop gardens (Figure 1). Broader research goals from this work were to improve connections between pollinators and urban planning and

landscape design. In this work I also aim to contribute to a culture of conservation among home- and building owners using pollination services by bees and pest controlling services by wasps as a focal point in outreach.

To sample bee and wasp populations for study, a single nest box was deployed at each location and monitored with citizen scientists who's assistance was requested through various presentations and web-based initiatives (Appendix A). There are myriads of nest box design types (reviewed in Appendix B), but in this study a single type was built consisting of 30 cardboard paper tubes 15cm in length (10 of each of three different tube widths; 3.4mm, 5.5mm, 7.6mm) fitted into a 10cm width white PVC pipe (Figure 2). These were affixed to wooden stakes, fence posts or tree limbs, facing southeast and in full or partial sun. Each nest box was labeled (Figure 3) for identification and public awareness (only 4 of 600 nest boxes fell to vandals). Nest boxes were set up in April and taken down in October of each year, over three years. Each nest box was opened, the brood cells removed from each nesting tube and stored over the winter in a cold room kept at 4°C. In spring, brood were moved into an incubation chamber at 26°C and 65% relative humidity, where their emergence to adulthood was monitored and controlled. Upon emergence each individual was identified to species.

This dissertation is comprised of six chapters: an introduction, conclusion, and four original data chapters (Chapter 2-5). As well, a synthesis of the literature on research using nest boxes to sample bees and wasps is included as an appendix item. In Chapter 2, I examine the landscape and socioeconomic factors that directly or indirectly explain patterns in the diversity of cavity-nesting bees, wasps, and their parasites. Bees and wasps were active at nest boxes at different times of the year with many species co-occurring and competing for available nest sites and so in Chapter 3 I investigate the emergence timing of colonizers to understand seasonality and competition within the community and to improve rearing methods. The study was carried out across a large urban landscape and so it was not feasible to replace nest box nesting tubes

during the year. And so, at each site, if no suitable nesting tubes were available (e.g. all in use by other colonizers) some potential colonizers could have been excluded. As a result, I was interested in estimating whether key species of interest were present at sites where they were recorded as absent and in Chapter 4 a modelling approach is employed to estimate the occupancy probability of six different bee species. Finally, with increasing promotion and commercialization of nest boxes as tools to 'save bees', in Chapter 5 I address six hypotheses on the validity of nest boxes as tools in native bee conservation and suggest more effort is needed to link public education, design and maintenance.

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1.4 Figures

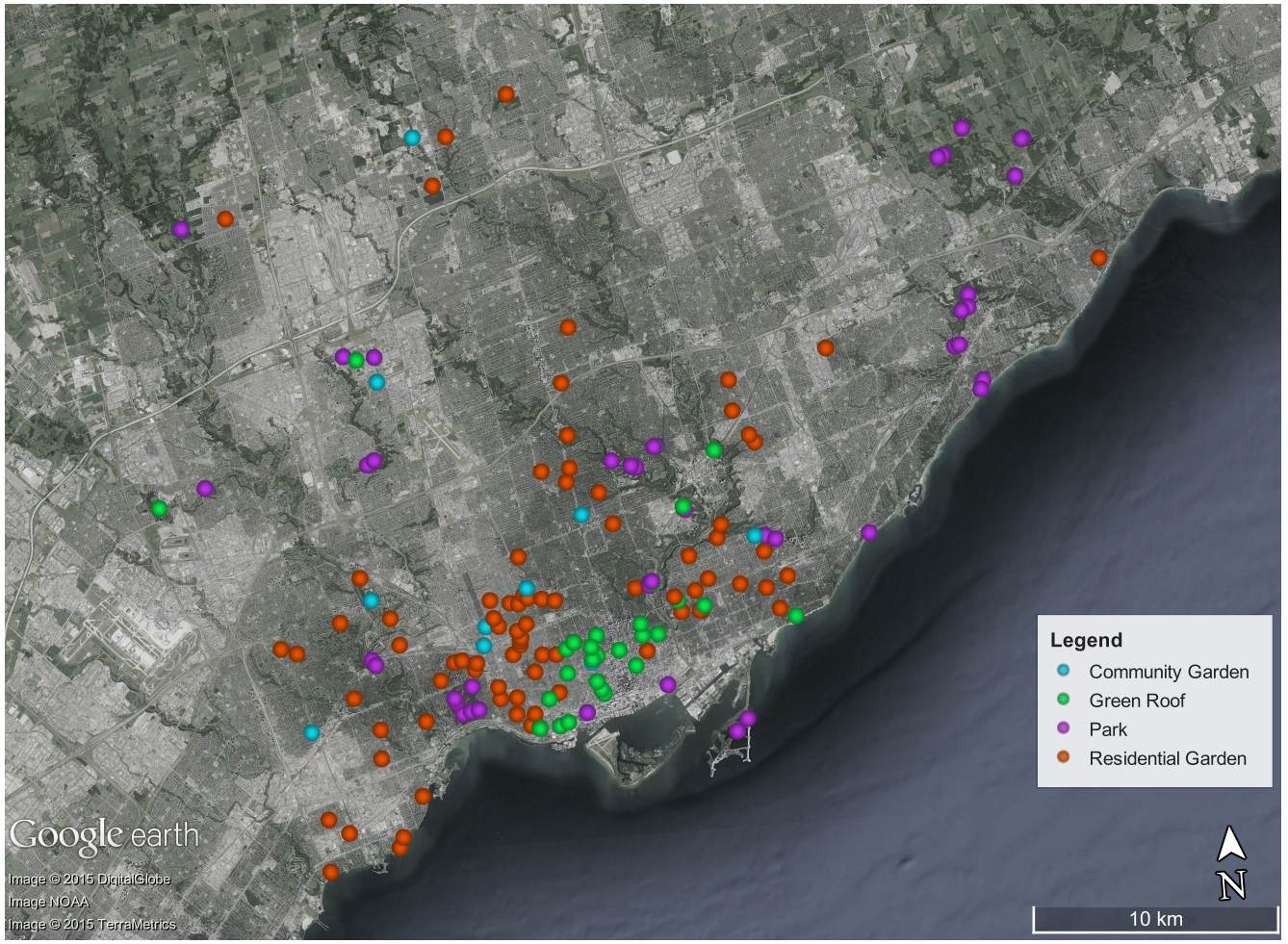

Figure 1. A topographic map of the city of Toronto showing the locations of the sites surveyed. Each site contained one nest box and was 250m from any other site.

Figure 2. The nest box design used to conduct the research study.

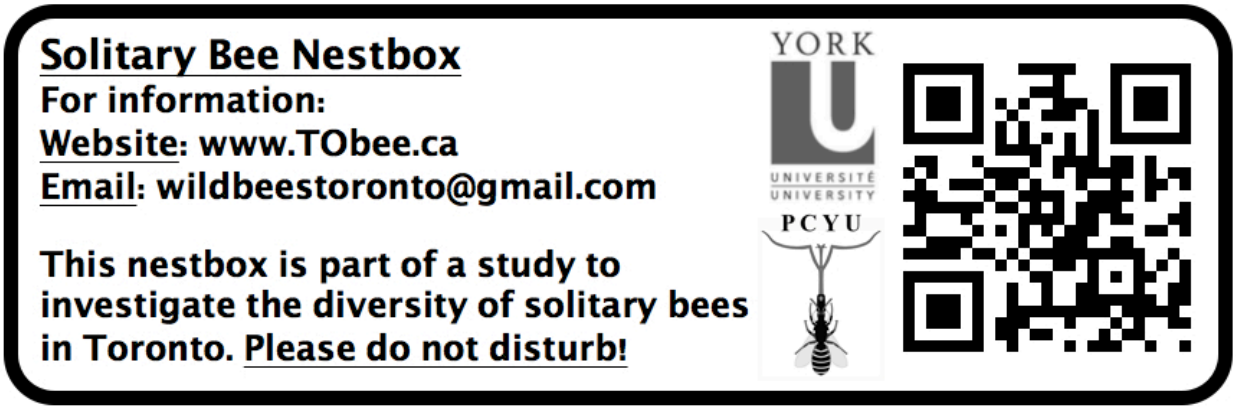

Figure 3. QR code and message attached to each nest box.

Chapter 2: Socioeconomic drivers of urban bee and wasp diversity

2.1 Abstract

Across cities, socioeconomic factors vary by neighbourhood and strongly influence the type, number, and maintenance of the urban green spaces they encompass. Socioeconomic factors might then also be important as indirect influences on patterns in the diversity and abundance of local species. In this study we use nest boxes to determine whether three socioeconomic factors (population density, mean household income, university education) were correlated with patterns of diversity and abundance of cavity-nesting bees, wasps, and their parasites. We include in the analyses indexes of habitat availability (HAI) – unique for each taxon analyzed – developed from high-resolution land use classification in the study region. From 200 nest boxes surveyed over three years, 84 species of bee, wasp, and parasite were recorded. Urban green space type and the HAIs were more important predictors of bee, wasp, and parasite populations than socioeconomic factors. However, wasps and parasites were significantly negatively correlated with increasing population density. Also, with all taxa combined, and when bee abundance was examined separately, there was a significant positively correlation with mean household income; leading to the first example of beneficial insects responding indirectly to the 'luxury effect'. These factors and the influence on urban biodiversity require more study. Promoting these – to some people – more meaningful connections between everyday life and bee and wasp populations could also inspire more urban citizens to care for wildlife in cities.

2.2 Introduction

As the majority of people live in cities, most of our experience with wildlife occurs in an urban context (Miller, 2005). In cities, wildlife is unequally distributed across the landscapes (Turner et al. 2004) and measuring its responses to urban environmental change - or lack thereof - can inform biodiversity conservation (McKinney, 2006; Fuller et al. 2008; Matteson & Langellotto, 2011; Werner, 2011). Those interested in studying biodiversity in cities often sample along an urbanization gradient (French et al. 2008; McDonnell & Hahs, 2008), where land use varies from rural to urban (Shochat et al. 2006), and where increasing distance away from the urban core is assumed to indicate decreasing human impacts (Blair, 1996). However, different cities expand in different ways and even the same city might expand differently and in different directions (Ramalho & Hobbs, 2012). Human population density similarly expands in non-linear ways. Urban regions have areas where human population densities are low (e.g. industrial areas) and where they are high (e.g. planned residential subdivisions, condo developments) (Gordon & Richardson, 1997). Accounting for population density – or how close people live together – could be an important demographic factor to consider when interpreting patterns in wildlife sampling (Kinzig et al. 2005; Evans et al. 2007). For example, as density increases so will infrastructure including housing, transportation, and associated impervious surfaces, which negatively impacts biodiversity (Frazer, 2005). City neighbourhoods can be further defined by a myriad of socioeconomic factors not commonly considered in analyses of urban biodiversity, including legacy effects (Boone et al. 2012): educational levels (Martin et al. 2004), lifestyle and social status (Grove et al. 2006; Troy et al. 2007; Grove et al. 2014), and other economic differences (Grove et al. 1997; Savard et al. 2000; Hope et al. 2003; Lowry Jr. et al. 2012; Cook et al. 2012; Clarke & Jenerette, 2015).

Bees are increasingly studied in urban environments because they are charismatic, important pollinators of flowering plants (Hernandez et al. 2009; Packer, 2010; Hennig & Ghazoul,

2011; Ollerton et al. 2011; Threfall et al. 2015) and in decline (Burkle et al. 2013; Ollerton et al. 2014; Kerr et al. 2015). Bees are ecologically diverse, and species respond differently to urbanization (Cane et al. 2006; Matteson & Langellotto, 2010; Winfree et al. 2011; Braaker et al. 2014; Harrison & Winfree, 2015). Furthermore, contrasting patterns in urban bee diversity have been found from studies in different cities. In New York, Fetridge et al. (2008) found the bee fauna in suburban gardens to resemble that of a local nature reserve, with a complimentary study reporting lowest diversity nearer the city core (Matteson & Langellotto, 2010). Using the proportion of impervious surface derived from land cover data, Arhné et al (2008) found that bumblebee species richness declined with urbanization in Stockholm City, Sweden, and Threfall et al. (2015) found decreasing bee richness and abundance with urbanization in Melbourne, Australia. Similarly, Banaszak-Cibicka & Żmihorski (2012) found that bee diversity declined with increased urbanization (as measured by the proportion of available green space) in Poznań, Poland. On the other hand, Kearns & Oliveras (2009) reported no negative correlation between bee diversity and two measures of urbanization in Boulder, Colorado. A study of 10 UK cities found no difference in the diversity of bees between urban and non-urban sites, but did not delineate degrees of urbanization (Baldock et al. 2015), and in Lyons, France, Fortel et al. (2014) recorded increasing bee diversity with increasing proportion of impervious surface. The lack of consistency among these studies could partly result from their using different proxies for urbanization. A classification system that can interpret urban green space and infrastructure at fine scales, in any urban environment, might provide more precise patterns regarding how bees and other wildlife respond to urban land use change (Mathieu et al. 2007; Wu et al. 2008; Thapa & Murayama, 2009; Zhou et al. 2010; Zhou et al. 2014).

Human preference for certain landscape conditions can remove resources for some species and increase them for others (Bolger et al. 2000; Gaston et al. 2005; Faeth et al. 2005; Hunter & Hunter, 2008; Fuller et al. 2008). Where finances permit, people can increase or

decrease plant diversity through gardening and landscape management (Gaston et al. 2005; Grove et al. 2006; Zhou et al. 2009; Nilon, 2011), although these effects are generally unlikely to be conscious. Subsequently, income levels may have an indirect impact on pollinators (Pawelek et al. 2009; Garbuzov & Ratnieks, 2014). In one study, Hope et al. (2003) found that urban plant diversity within 900m^2 was positively correlated with mean household income. The authors termed the relationship between income and species diversity – the 'luxury effect', and this pattern has been found in several subsequent studies in different cities (Martin et al. 2004; Lowry Jr. et al. 2012; Clarke & Jenerette, 2015). The 'luxury effect' is less resolved for non-plant taxa. For example, Loss et al. (2009) found no relationship between household income and bird diversity except for an increase in the number of exotic species in richer areas. In another study, Lerman et al. (2012) found bird and plant diversity, but not that of insects, increased in neighbourhoods of higher mean household income. Grove et al. (2014) suggests that the 'luxury effect' is not sufficient to directly explain patterns in urban wildlife. Rather, the 'ecology of prestige' whereby patterns in household expense on gardening are motivated by group identity and social status, not income levels, is more important and reflects both socioeconomic and demongraphic factors (Troy et al. 2007; Grove et al. 2014). Nevertheless, more studies are needed to elucidate how socioeconomic factors in cities are implicated in impacting beneficial insects, such as pollinators and the important services they provide (Vanbergen et al. 2013).

In this study, we assess the impacts of socioeconomic, demographic, and landscape factors on urban populations of bees, wasps, and their parasites. To survey populations we use nest boxes, which provide nesting habitat for cavity-nesting species (Krombein, 1967; Taki et al. 2004; Sheffield et al. 2008; Lee-Mader et al. 2010; Martins et al. 2012; MacIvor & Packer, 2015). To assess local habitat availability, we developed a habitat availability index (HAI) based on HERCULES (High Ecological Resolution Classification for Urban Landscapes and Environmental Systems) land use classifications (Cadenasso et al. 2007). This is a flexible classification system

that quantifies different categories of land type from visual interpretation of aerial maps (Zhou et al. 2010).

As local landscape conditions are important for habitat availability and biodiversity patterns of urban bees (Tommasi et al. 2004; Holzschuh et al. 2007; Matteson & Langellotto, 2010; Matteson et al. 2013; Braaker et al. 2014), we first hypothesized that the habitat availability index (HAI) would be positively correlated with nest box abundance. Through the HAI, this is the first study to utilize the HERCULES classification categories to analyze patterns in urban insect populations. Second, as flowering plant diversity is correlated with increasing urban bee diversity (Hernandez et al. 2009; Kearns & Oliveras, 2009), and generally increases with mean household income (Hope et al. 2003; Kinzig et al. 2005), we hypothesized that bee diversity would respond positively to increasing mean household income. Lastly, since species richness generally declines with increasing human population density (Cincotta et al. 2000; Tratalos et al. 2007; but see Lowenstein et al. 2014) we hypothesized that nest box colonizer diversity would be negatively correlated with human population density.

2.3 Methods

2.3.1 Nest boxes

To sample cavity-nesting bees, wasps, and their parasites, 200 nest boxes were set up as described in Chapter 1.

2.3.2 Landscape factors

Each nest box was set up in one of four ‘site types’ delineated by ownership and management regime: residential gardens, community gardens, city parks, and building rooftops. Residential gardens were either front- or backyards that occurred on privately owned property and were maintained by a homeowner. Community gardens were located in a publicly accessible space e.g.

in a neighbourhood park, the grounds of an apartment complex, or in a hydro corridor, where groups of people gardened collectively. Urban parks were contained within the boundaries of named parks, as designated by the City of Toronto and the Toronto and Region Conservation Authority (TRCA). These are usually grassy areas with sparse tree cover but usually with planted flowerbeds around the edges or along paths (Gilbert, 1989). Building rooftops were atop single buildings upon which vegetation (e.g. planters, green roofs) had been installed. Green roofs are increasingly common in Toronto where they are mandatory on new buildings of certain types and enforced with a construction standard (Torrance et al. 2013).

The location of each site was mapped in Google Earth Pro and a buffer of 200m in radius was overlain onto each using the plug-in program RINGS (Metzger + Willard, Inc., Tampa, Florida). This radius was selected based on other studies (e.g. Dauber et al. 2004) and because most solitary bee species forage at distances below 200m (Zurbuchen et al. 2010a). The area within the buffer was estimated for each of the categories in HERCULES using visual assessment (Cadenasso et al. 2007; Zhou & Cadenasso, 2012) (Figure 4; Table 1). Five land use categories were identified based on HERCULES: (1) coarse-textured vegetation (trees and shrubs), (2) fine textured vegetation (herbs and grasses), (3) bare soil, (4) pavement, and (5) buildings (Table 1). To these, we added a sixth and seventh category, each important for our study region: 'vegetated roofs' and water bodies. Using visual interpretation and the custom polygon function in Google Earth Pro, the proportion of area within the buffer around each site was estimated for each of the seven categories (Cadenasso et al. 2007; Zhou & Cadenasso, 2012). The area calculated for each land use type was transformed into a categorical variable as in HERCULES (Cadenasso et al. 2007). Thus, 0 = 0% of the buffered region belonged to that habitat type, 1 = 1 to 10%, 2 = >10% to 30%, 3 = >30%-50%, 4 = >50%. The habitat availability index was then calculated as:

$$HAI = \sum_{n=1}^{C} (\mathrm{R} * \mathrm{W})$$

Where C is the number of HERCULES habitat classification categories, R is the ranking from 0-4 based on HERCULES (Cadenasso et al. 2007) and W is the weighting multiplier: the correlation coefficient between the measurement of the taxon of interest (e.g. species richness, abundance, diversity) and the proportion of area of the classification category within 200m radius around each nest box (Table 2). Weighting multipliers could be positive or negative depending on the direction of the correlation between the classification category and the taxa of interest. HAIs are therefore a measure of habitat availability specific to the taxa of interest and independent of habitat classification category diversity.

2.3.3 Socioeconomic factors

Socioeconomic factors were obtained from the most recently available city of Toronto census data, which are delineated by neighbourhood (City of Toronto Demographics, 2011) (Table 3). A neighbourhood in the most basic sense comprises a clearly bounded territory (defined by the City of Toronto), with streets and services, generating space for social networking (Kallus & Law-Yone, 2000). From the census data available, we selected three socioeconomic factors presumed to have indirect impact on nest box colonizers. These factors included mean household income (in $ Cdn), the proportion of the citizenry that was university-educated, and human population density (per km^2) (Table 3). 'Site' was assigned a value for each of these three variables based on the neighbourhood in the city in which the nest block was located.

2.3.4 Analysis

To determine the role of socioeconomic factors in describing the variation in patterns in cavity nesting bee, wasp, and parasite populations in the nest boxes, step-wise model selection following the Akaike information criterion (AIC) (Burnham & Anderson, 2004) was used. The factors included were urban green space "site" type, the habitat availability index (HAI), mean

household income, human population density, and the proportion of households occupied by people with university-level education. To examine differences in bee and wasp genera having different habitat requirements, abundance data for bees, *Osmia* (Megachilidae), *Megachile* (Megachilidae), *Hylaeus* (Colletidae), and wasps *Symmorphus* (Vespidae), *Trypoxylon* (Crabronidae), *Passaloecus* (Crabronidae), were analyzed genus by genus. Factors deemed important from model selection for each of the taxa examined were analyzed using multiple regressions to determine any significant influences (α=0.05) on trends in diversity and abundance across sites. These analyses were completed using R Studio statistical program v0.98 (R Core Team, 2014). Lastly, in the R package 'vegan' (Oksanen, 2015), a canonical correspondence analysis (CCA) was used to ordinate species-level responses to the socioeconomic factors and the HAI determined for total colonizer abundance, to discover any outlier species or clustering among groups of taxa that might provide additional detail about patterns over that detected from model selection and multiple regression.

2.4 Results

From the entire sample, a total of four insect orders and 84 species in 43 genera were identified (Appendix D). There were 75 hymenopteran species of which 19 (in 13 genera) were parasitoids and 5 were cleptoparasitic bees. The average number of larvae provisioned per nest box was 142.1±7.8, and when all occupants were combined the average species richness recorded per nest box was 7.7±0.3.

2.4.1 Site type

For all taxa combined, rooftops had significantly lower species richness, abundance, and diversity than did residential gardens, community gardens, and urban parks, which had no differences among them (Figure 5). Nest provisioning, non-parasitic wasps (see Appendix D) analyzed

independently followed this same trend for species richness and abundance, and only bee abundance was not significantly different between site types (Figure 5). Bee species richness was significantly lower on roofs, but urban parks were no different from any other site type (Figure 5). Parasite abundance was significantly higher in urban parks than all other site types with no significant variation among the remainder. For parasite species richness, the only statistically significant result was that rooftops had fewer species than any other site type (Figure 5).

2.4.2 Habitat availability

Total nest box species richness, abundance, and diversity all increased significantly with increasing habitat availability (Figure 6). Among bees, wasps, and parasites the habitat availability indexes were significantly positively correlated with abundances (Figure 7), and with species richness of wasps and parasites, but not bees (Appendix E). All wasp genera and two of the three bee genera examined (*Osmia* and *Hylaeus* but not *Megachile*) exhibited a significant positive correlation between abundance and their HAI (Appendix F). The weighting multiplier in the habitat availability indexes for building and pavement classification categories were negative for all taxa. For bee species richness and abundance, positive weighting multipliers were highest for fine vegetation (FV) (Table 2). For wasp and parasite species richness and abundance, the weighting multipliers were highest for coarse vegetation (CV) (Table 2).

2.4.3 Socioeconomic factors

Among the socioeconomic factors examined, mean household income levels were significantly negatively correlated with increasing human population density (e.g. Cook et al. 2012) and significantly positively correlated with increasing proportions of university-educated households (e.g. Hope et al. 2003; Zhou et al. 2009; Boone et al. 2010) (Figure 8). No correlation between the

proportion of university-educated households and human population density was evident (Figure 8).

For all taxa combined, species diversity and abundance but not species richness, increased significantly with increasing mean household income (Figure 6). Bee abundance examined separately also significantly increased with increasing mean household income (Figure 7). Nest-provisioning wasp abundance declined significantly with increasing population density (Figure 7). Human population density also had a strongly significant negative impact on parasite species richness (Figure 7).

2.4.4 Species-level responses

The canonical correspondence analysis (CCA) ordination was significant in explaining the variation in species abundance across the entire sample ($F=2.33$, $p=0.005$) (Figure 9; Appendix G). The first CCA axis explained 91.3% of the variation attributed to HAI and 70.3% of variation in human population density. The second CCA axis explained 76.7% of the variation resulting from the type of urban green space sampled. Less than 20% of the variation attributed to mean household income and the proportion of university-educated households was captures by the first two CCA axes. In general, the CCA demonstrated that response patterns attributed to HAIs and socioeconomic factors varied considerably within and between bee, wasp, and parasite groups (e.g. Figure 7), and contrasted between species, even within the same genus (Appendix G-H). For example, among *Megachile* bees, the following positive relationships between species and urban factors were found: *M. campanulae* (Robertson) (“Meg.camp”) abundance responded positively to human population density, *M. rotundata* (Fabricius) (“Meg.rot”) to rooftops and *M. centuncularis* (L.) (“Meg.cent”) to urban parks, and *M. pugnata* Say (“Meg.pug”) responded strongest to the HAI (Figure 9). Among *Trypoxylon* wasps, *T. frigidum* Smith (“Try.frig”) responded positively to proportion of university-educated households, but generally was widespread at all sites types, *T.*

lactitarse Saussure ("Try.lac") responded negatively to human population density, whereas *T. collinum* Smith ("Try.col") responded positively to the same variable (Figure 9). Most parasite species responded positively to the HAI and negatively to human population density (Appendix G-H).

2.5 Discussion

Bees, wasps, and their parasites respond significantly to local landscape factors that affect habitat availability (Steffan-Dewenter et al. 2002; Kennedy et al. 2011; Scheper et al. 2015; Harrison & Winfree, 2015). In cities, landscape factors are influenced by local socioeconomic conditions, further altering management of and attention to features that influence biological diversity (Pickett et al. 2001; Kinzig et al. 2005; Gobster et al. 2007; Matteson et al. 2013; Gaston et al. 2013; Grove et al. 2014). Overall, we found that urban bees, wasps, and their parasites respond significantly to the type of urban green space, with significantly less colonization on roofs versus the other site types surveyed. One exception was bee abundance, which did not differ among site types, presumably because of the high productivity of *Megachile* in nest boxes on rooftops (see MacIvor, 2015). With site type omitted from analysis, nest box abundance and diversity was positively correlated with habitat availability as well as household income levels, and negatively correlated with human population density (Figure 6).

Habitat availability indexes (HAIs) were significantly positively correlated with nest box colonization, and so we accepted our first hypothesis that habitat availability would be important for nest box colonizer abundance. Total nest box species diversity and abundance, especially that of bees, increased with increasing mean household income (Figure 6). We accept our first hypothesis: that these taxa would be positively correlated with the luxury effect, as predicted in Matteson et al. (2013) and empirically observed in urban plant communities (Hope et al. 2003; Kinzig et al. 2005; Clarke & Jenerette, 2015). Lastly, human population density was negatively

correlated with wasp and parasite abundance but not that of bees, and so our third hypothesis, that nest box abundance would be negatively correlated with increasing human population density, is partially supported (Figure 6-7). However, response to habitat availability and socioeconomic factors varied among genera (Appendix F) and species within each of our biological categories (Appendix G). These data suggest both socioeconomic and demographic factors need to be included in studies examining patterns in urban biodiversity, which to date largely use landscape variables only in interpretation. In the following sections we discuss the significance of each factor and their impacts on patterns of bees, wasps, and parasites.

2.5.1 Site type

For all nest box inhabitants, there were no significant differences in diversity or abundance among urban green space types, except that rooftops were significantly less colonized. Rooftops are vertically isolated from all other habitat types (which were at ground level), posing a physical impediment to nest box discovery by potential occupants (MacIvor, 2015). Physical barriers have been shown to impede movement of pollinators (hedgerows; Krewenka et al. 2011), but another study found both a river and large roadway to be passable by foraging bees (Zurbuchen et al. 2010b). However little is known about how buildings and other urban infrastructure impact movement (Westrich, 1996; Chapman et al. 2003; Braaker et al. 2014). More study is needed to identify the habitat value of rooftop gardens as no two roofs are the same (Oberndorfer et al. 2007), the number of installations are increasing in cities around the world, and their usefulness as habitat for wildlife is impacted by design and surrounding landscape conditions (Tonietto et al. 2011; Torrance et al. 2013; Williams et al. 2014). Whether there are “critical mass” effects whereby bee diversity on rooftops can be maintained at levels similar to those at ground level needs to be established. Appropriate design to foster such diversity also needs to be assessed.

Our observation that there is no difference in cavity-nesting bee abundance between urban green space types is presumably in part a guild-level response, as certain cavity-nesting species are abundant in urban landscapes because of nesting opportunities created in gardening and in infrastructure, including buildings (Westrich, 1996; Cane et al. 2006). Pereira-Peixoto et al. (2014) surveyed nest box colonizing bees and wasps along an urbanization gradient and found highest species richness at the urban-rural interface compared to urban or rural only. The authors suggest that some species may benefit from the combination of abundant nesting resources in urban gardens and more abundant prey in nearby parks and forests. The distance to proximal forested area is likely important but the impact of ths upon urban Hymenoptera requires additional study (Fortel et al. 2014).

2.5.2 Habitat availability

Total nest box species richness and diversity were significantly positively correlated with the habitat availability indexes (Figure 6). Independent analysis of bee, wasp, and parasite groups all indicated that species richness and abundance were significantly positively correlated with HAIs (Figure 7; Appendix E). Among all genera examined, the trend was strongest in spider-collecting *Trypoxylon* wasps (Appendix F) and ordination showed other spider-collecting species (e.g. *Dipogon sayi* Banks) responded similarly, as did vespid wasps including *Symmorphus*, *Ancistrocerus*, and *Euodynerus* species (Appendix G). Presumably this is a result of wasp prey being more closely associated with resources in or adjacent to forests dominated by complex vegetation including shrubs and trees (e.g. tree katydids for *Isodontia mexicana* Saussure; leaf-feeding caterpillars sought by *Symmorphus* spp.). Among classification categories that formed the HAI index, the category that included complex vegetation dominated by shrubs and trees [complex vegetation (CV)] was weighted the highest for *Trypoxylon*. Coudrain et al. (2013) also found the abundance of *Trypoxylon figulus* to be significantly positively correlated with

increasing forest cover and forest edge habitat. Parasite richness and abundance were also significantly positively correlated with the HAI.

With the HAIs, we demonstrate that differentiating between different kinds of green space (e.g. coarse and fine vegetation, bare soil) and urban impervious surface (e.g. buildings, pavement) can be useful in interpreting patterns in hymenopteran diversity, and illustrates the importance of landscape ecology in the study of urban environments (Breuste et al. 2007). Most studies examining local landscape factors affecting bee diversity in cities include in their analysis the type of green space studied and the proportion (%) of impervious surface or green space within the sampling area. The HAI includes both and can be quantified from any urban landscape using freely available mapping software (e.g. Google Earth Pro, Bing Maps). Since bees, wasps, and parasites all responded strongly in analysis to the HAI and the index is weighted depending on the response of each taxon of interest to each classification category in the HAI, the index could be used in cities around the world to improve generalizations made about how pollinators and other animals respond to urbanization.

2.5.3 Mean household income

The general increase in plant diversity with household income - the ‘luxury effect’ (Hope et al. 2003) - could explain the observed correlation between bee abundance and household income (e.g. Pawelek et al. 2009; Matteson & Langellotto, 2010; Pardee & Philipot, 2014). Urban gardeners are increasingly interested in developing habitat for pollinators by setting aside space for nesting activity and/or planting flowers attractive to bees (Garbuzov & Ratnieks, 2014). However, the link between household income and homeowner participation in activities to enhance native biodiversity is not well researched, and participation is likely driven moreso by lifestyle choices and social status (Grove et al. 2014). For example, one study found that middle class income homeowners were the most receptive to native plant landscaping initiatives, but

most strongly impacted by what they perceived their neighbours to prefer (Peterson et al. 2012). In another study of backyard bird-feeding activity, Davies et al. (2012) found no effect of income levels, but rather, a positive correlation between bird visits and property size and with age of the head of the household.

Our findings indicate all cavity-nesting bees but only some wasps and parasites responded indirectly to the luxury effect (Figure 9). Wasps that collect hyper-abundant invertebrates as prey would presumably find these in most urban habitats containing coarse vegetation (CV); for example, *Trypoxylon* wasps hunt spiders that are common and widespread (Shochat et al. 2004). The biodiversity variables for these wasps were not correlated with mean household income. Similarly, Loss et al. (2009) found no effect of income levels on bird diversity. Clarke & Jenerette (2015) also found increasing plant species richness in areas of higher household income, but as a result of increased inclusion of ornamental plants in the gardens of the rich. Mixed responses of different taxa indirectly to mean household income are potentially due to the singular conception of the luxury effect: it is based solely on income, and other related factors such as ethnicity, culture, and lifestyle forming the 'ecology of prestige' are ignored (Grove et al. 2006; 2014). Additional study of indirect impacts of household income and income-related factors on local biodiversity is required.

2.5.4 Human population density

Human population density was significantly negatively correlated with total species richness, but no effect was apparent for abundance or diversity in nest boxes. Bees examined independently were not impacted by human population density, however nest provisioning wasp species richness and abundance, and parasite species richness were significantly negatively affected (Figure 7; Appendix E). Some positive correlations with human population density occurred, but

only *Trypoxylon* wasps increased significantly (Appendix G), with ordination showing the trend driven by the common, *T. frigidum* and *T. collinum* (Figure 9).

Other studies have found wildlife abundance and diversity to decline with increasing human population density: Luck (2007) reviewed empirical literature on human population density and impacts on biodiversity and found that 77% of 22 studies reported a negative relationship. Among non-plant taxa, both lizards (Germain & Wakeling, 2001) and birds (Turner et al. 2004; Strohbach et al. 2009) have been shown to decline significantly with increasing population density. However, Lowenstein et al. (2014) found in a survey of 25 urban gardens in Chicago that increasing human population density resulted in higher abundance and diversity of bees. These authors surmised that that was due to there being more private residential gardens in more densely occupied areas and that these provided both nesting and foraging opportunities for bees. These gardens can also support beneficial wasps such as those in the genus *Passaloecus*, which are predators of aphids and were abundant in our study. Aphids are pests that can increase in abundance with increasing urbanization (Denys & Schmidt, 1998) and attack many plants grown in home and community food gardens (Pirone, 1978; Dreistadt et al. 2004). For example, one study examining stressors on urban Oak trees found aphids and their lacewing predators to be more prevalent in managed city gardens compared to a nearby University campus (Cregg & Dix, 2001). Residential garden owners in densely populated areas might benefit from nest boxes set up to enhance aphid-collecting wasps to regulate pests on crops and other cultivated plants (Mackauer & Völkl, 1993).

2.5.5 Conclusions

In this study we show that patterns in nest box colonization by bees wasps and parasites are strongly influenced by the type of urban green space and the local availability of habitat. Socioeconomic factors were also important for nest box colonizers. Bee abundance responded

positively to the mean household income, whereas nest provisioning wasps and parasites responded negatively to human population density. However, even among species within a genus, contrasting patterns in response to different socioeconomic factors were evident (Figure 9). More studies should utilize freely available socioeconomic data to interpret trends in urban wildlife and inform urban design (Luck et al. 2009; Cook et al. 2012; Cadenasso et al. 2013). Linking interactions between socioeconomics, demongraphic, and ecological patterns could provide new ways to promote conservation science among citizens and through policy in cities, by connecting biodiversity and ecosystem services to everyday factors not normally considered in its promotion and management.

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2.7 Tables

Table 1. List of land use categories defined in the HERCULES model used in the development of the habitat availability index (HAI).

Habitat Category	Acronym	Notes
Course Vegegtation	CV	Tree and shrub dominated; shading ground
Fine Vegetation	FV	Open, sunned ground vegetation; dominated by wildflowers, grasses (incl. cultivated crops)
Bare Soil	BS	Open ground surface with sparse vegetation; soils provide nesting materials for cavity-nesters
Vegetated Roof	VR	Open, sunned rooftop gardens containing short growing vegetation: grasses and wildflowers but limited nesting opportunities
Building	B	Infrastructure of all kinds, vegetation on balconies or windowsills; opportunities for nesting in brick and mortar and other holes
Pavement	P	Hard, impervious surfaces: roads and sidewalks
Water	W	No nesting or foraging opportunities

Table 2. The correlation coefficients for each of the taxa examined independently for each of the classification categories that comprise the HAI.

	Taxa	CV	FV	W	BS	P	B	GR
Species Richness	Bees	-0.015	0.045	-0.001	0	0.004	0	0.017
	Wasps	0.136	-0.004	0.060	0.007	-0.169	-0.165	-0.046
	Parasites	0.042	-0.005	0.001	0	-0.021	-0.039	-0.010
	Total	0.034	0.002	0.007	0	-0.044	-0.067	-0.039
Abundance	Bees	-0.014	0.040	-0.010	0	0.013	0	0.029
	Wasps	0.068	-0.001	0.038	-0.001	-0.088	-0.091	-0.054
	Parasites	0.024	0.001	0.010	0	-0.007	-0.045	-0.007
	Total	0.001	0.023	0	0	-0.002	-0.028	0.001
	Osmia	-0.003	0.044	-0.014	-0.001	0	0.002	0
	Megachile	-0.006	0.010	0	0.004	0.010	-0.001	0.106
	Hylaeus	-0.024	0.005	0	0.026	0.018	0.006	-0.005
	Trypoxylon	0.004	0.007	0.003	-0.005	-0.030	-0.006	-0.051
	Passaloecus	-0.021	0.024	-0.010	-0.011	0.012	0.012	0
	Symmorphus	0.101	-0.021	0.130	0	-0.113	-0.142	-0.011
Shannon Index	Total	0.058	0.001	0.019	0.002	-0.090	-0.088	-0.114

Table 3. The socioeconomic and habitat availability factors considered in the analysis of the nest box populations. HAI represents the habitat availability index (see equation in Methods section).

Socioeconomic Factors	Mean	Range	St. Dev.	Source	Notes
Human population density (/km^2)	5,841	978 -21,180	3,588	City of Toronto Demographics, 2011	Total number of people in the neighbourhood.
Education level (%)	73%	42% - 90%	12.3%	City of Toronto Demographics, 2011	Percentage of people living in the neighbourhood with a University degree.
Average Household Income ($)	$82,340	$41,032 – $313,939	$49,659	City of Toronto Demographics, 2011	The amount of income in dollars earned per household per year.
Habitat Availability Factors	Mean	Range	St. Dev.	Source	Notes
HAI	4.50	1.75 – 6.50	0.92	Visual interpretation of Google Earth imagery	Index of habitat availability using HERCULES (Cadenasso et al. 2007)
Built Area (%)	20%	0 – 60%	15.1%	City of Toronto land use database in ArcGIS	Proportion of building footprint within the 300m radii sampling area

2.8 Figures

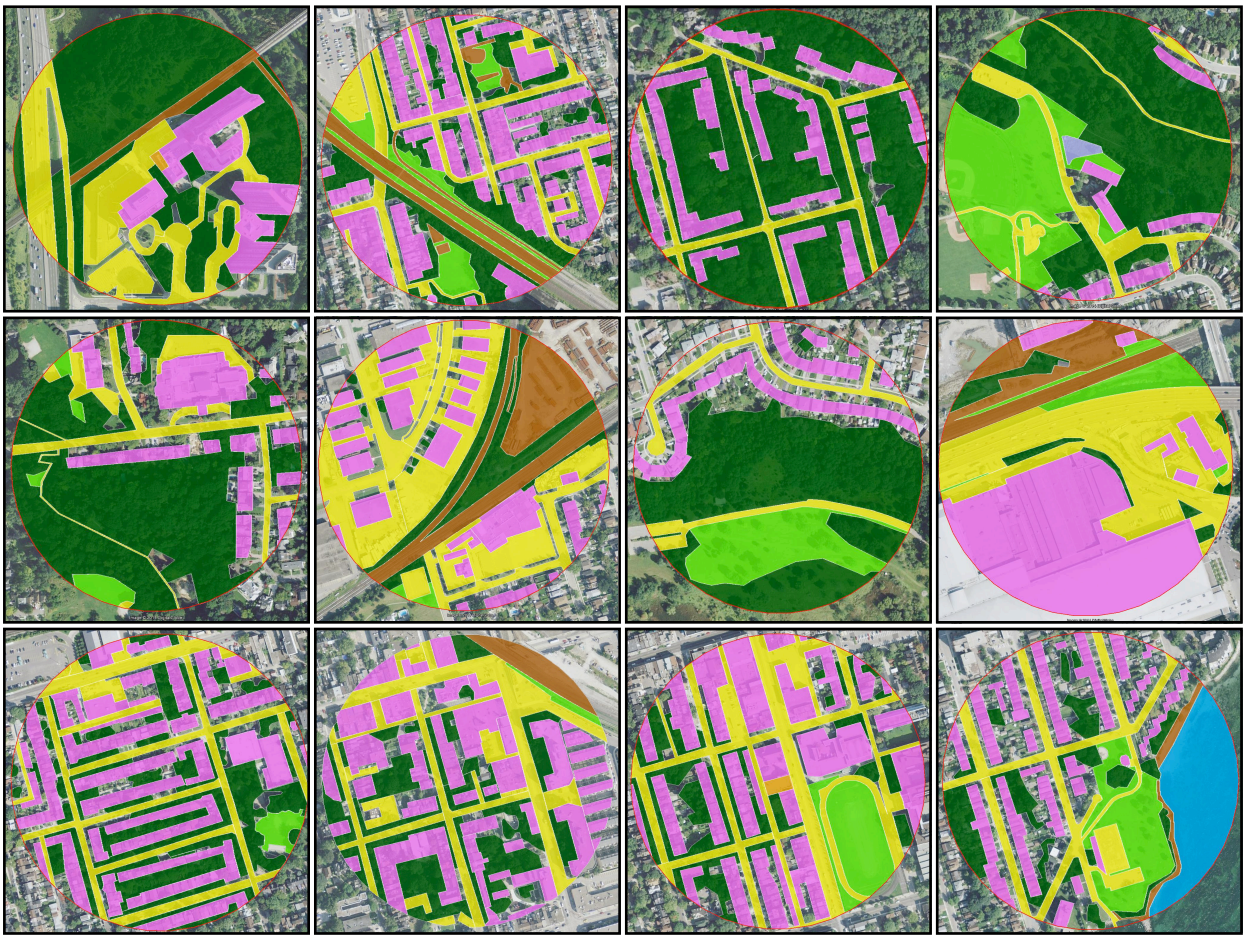

Figure 4. A representation of sites mapped using the HERCULES land use classification system (Cadenasso et al. 2007). In these examples, yellow = pavement, pink = building, light green = fine vegetation, dark green = coarse vegetation, light purple = vegetated roof, brown = bare soil, blue = water.

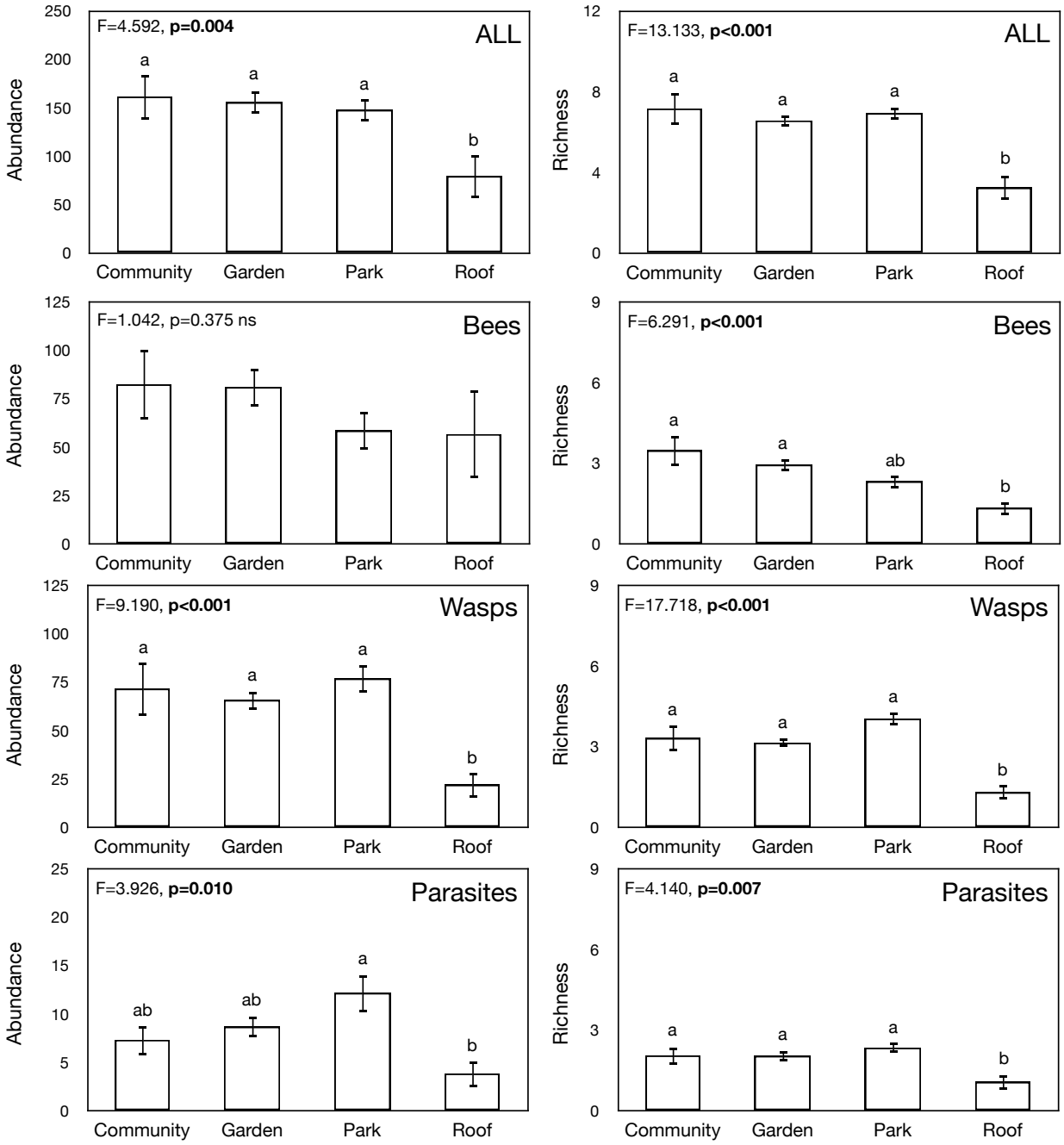

Figure 5. Differences in abundance and richness values by urban green space type, for all specimens total, and for bees, wasps, and parasites. Site types included community gardens (N=19), residential gardens (N=85), urban parks (N=56), and rooftops (N=30). Significant differences between sites were annotated alphabetically.

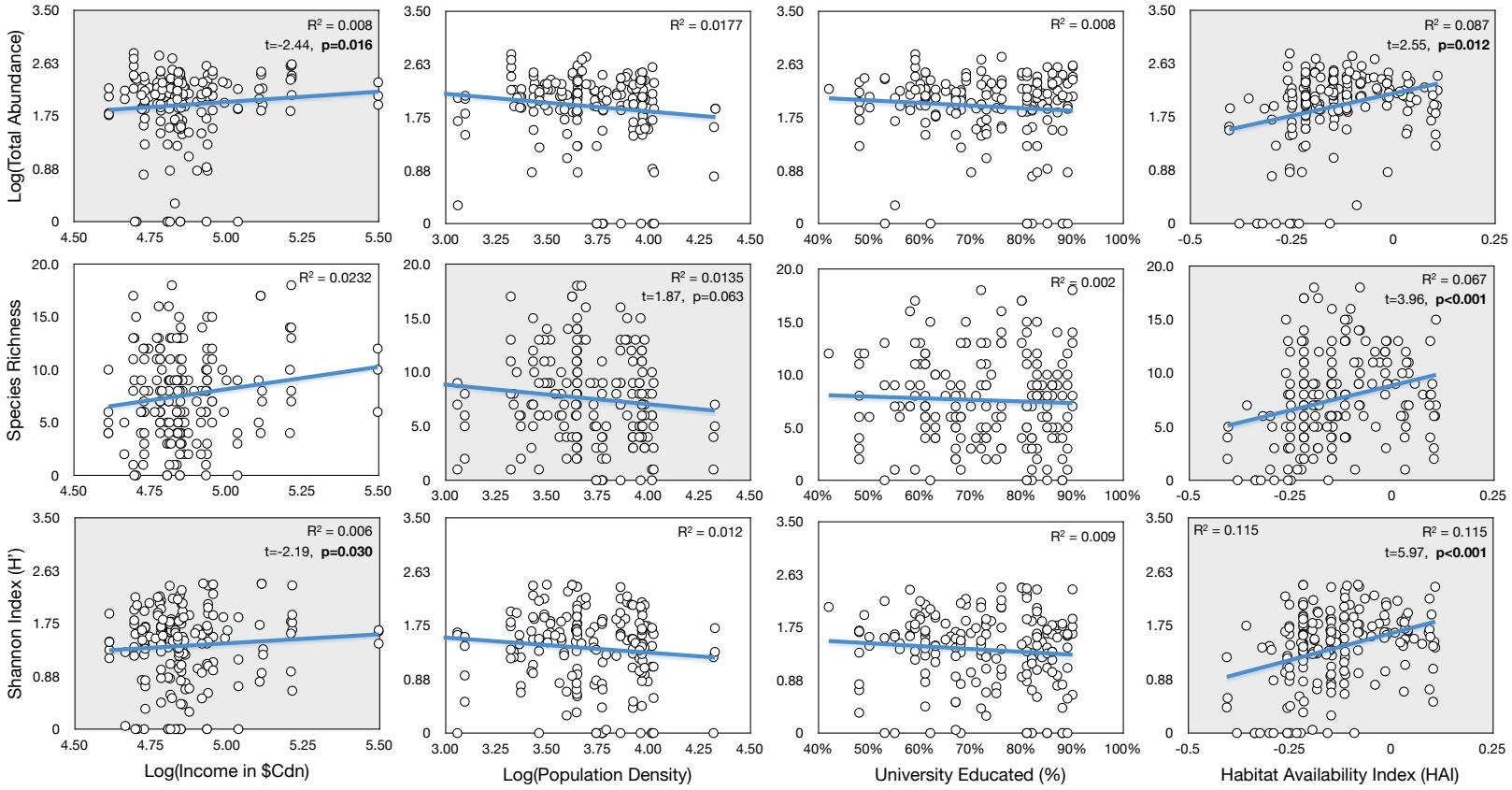

Figure 6. Socioeconomic factors influencing abundance, species richness, and Shannon index of diversity when all specimens were combined. Scatterplot boxes shaded grey included those factors that were identified in the top model equation for each colonizer group. A bolded p-value identifies those factors that had a significant effect on the observed data.

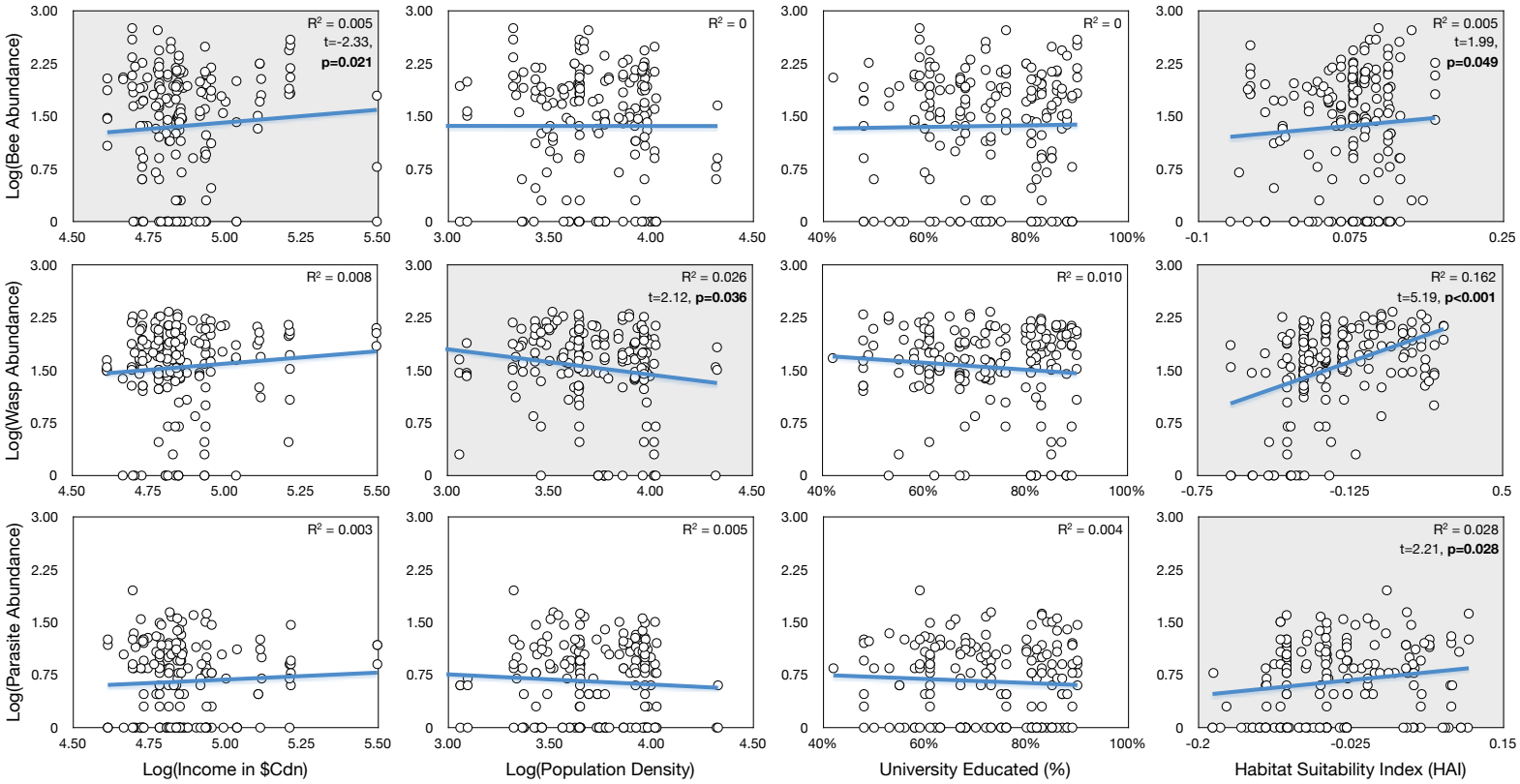

Figure 7. Socioeconomic factors that influence bee, wasp, and parasite abundance. Scatterplot boxes shaded grey included those factors that were identified in the top model equation for each colonizer group. A bolded p-value identifies those factors that had a significant effect on the observed data.

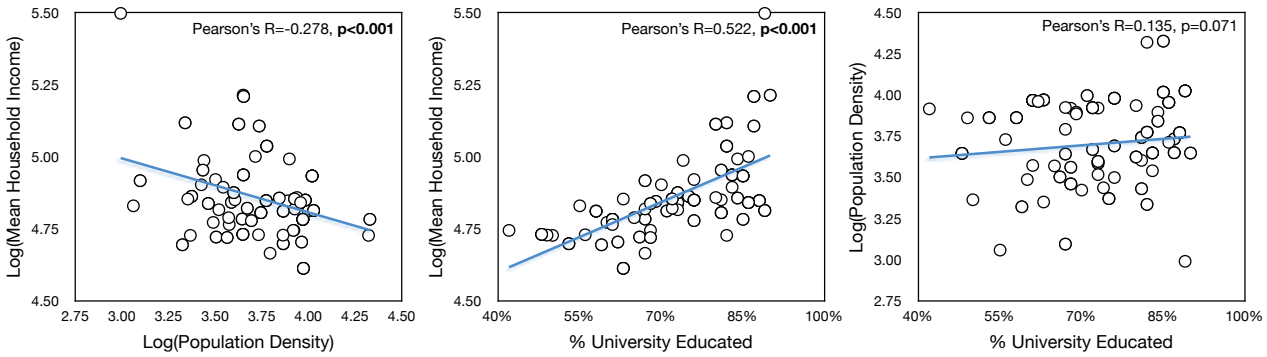

Figure 8. Pearson' R correlations for the three socioeconomic factors investigated: mean household income, human population density, and the proportion of university-educated households. Significant correlations are shown where p-values are bolded.

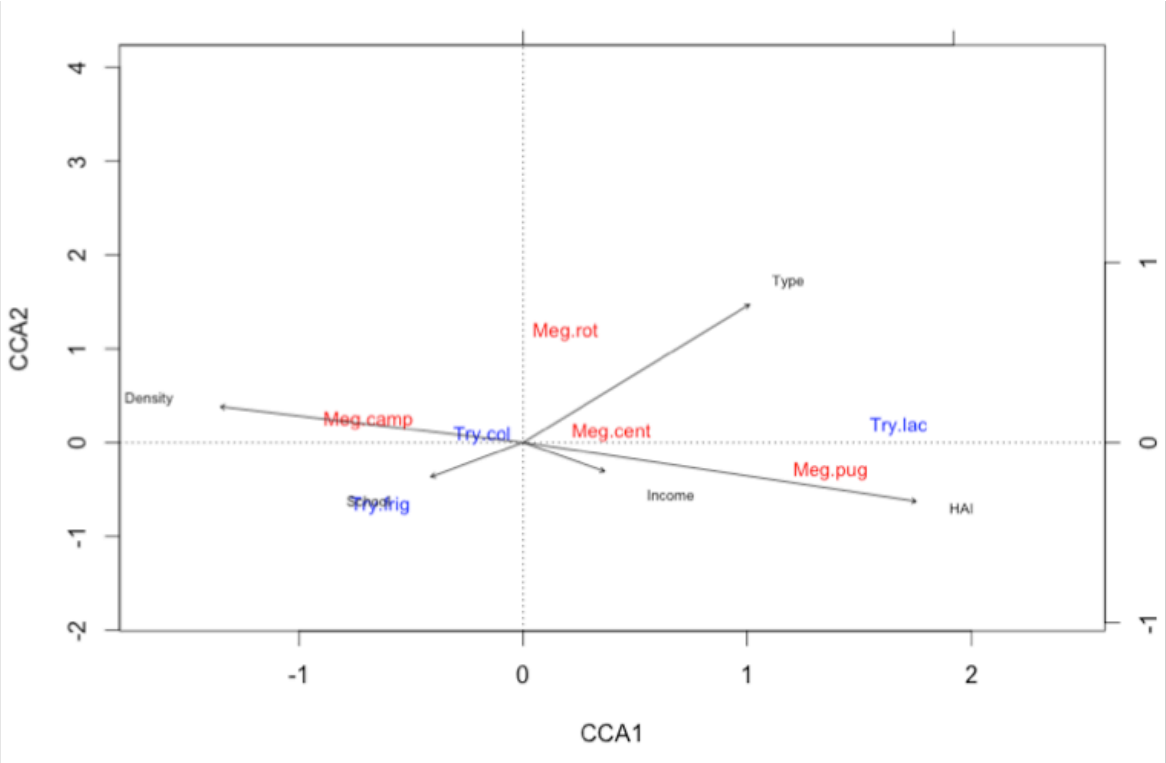

Figure 9. Canonical Correspondence Analysis (CCA) illustrating the responses of some of the most common bee and wasp species to the socioeconomic factors and the index of habitat availability. Bees are labeled in red, nest provisioning wasps in blue.

Chapter 3: Emergence timing and overlap in a community of cavity-nesting bees and wasps

3.1 Abstract

Incubating and rearing cavity-nesting bees, wasps, and parasites from nest boxes to track emergence timing can contribute additional information regarding their seasonality, co-occurrence, and partitioning of resources. Two hundred nest boxes were set up over three years to survey populations of bees, wasps, and their parasites in a large urban landscape. All brood cells collected at the end of each year were kept in cold storage than incubated in the spring to determine species identity and the length of the incubation period. The time to emergence of 47 species of bee, wasp, and parasite species ranged from 0 to 38 days, with Mason bees (*Osmia* spp.) emerging from nests within the first two days and the tropical-in-origin *Megachile sculpturalis* Smith emerging significantly later than all other species. In general, intraspecific emergence times were highly conserved and many significant differences existed between species over the incubation period. There were no differences in the variation in emergence time between earlier and later emerging species. Interspecific mean day to emergence time increased significantly with increasing body size. In addition, there were no differences in emergence time between native and introduced species. Interpreting and comparing emergence times can illustrate seasonality among co-occurring species using similar niches, and can better inform conservation of species that use artificial nest boxes.

3.2 Introduction

Niche partitioning between ecologically similar species is an evolutionary adaptation to minimize resource overlap and competition (Richards, 1927; Schoener, 1974; Albrecht & Gotelli, 2001; Martin et al. 2004; Taylor et al. 2014). For example, many bee and wasp species have similar nesting requirements but have evolved to partition resources spatially (Willmer & Corbet, 1981; Tylianakis et al. 2005), diurnally over a foraging day (Hoehn et al. 2008) or phenologically over a flight season (Wcislo & Cane, 1996). While some social bees and wasps are active over long periods during the year (Inouye, 1978; Packer, 1986; Fussell & Corbet, 1991; Potts & Willmer, 1997), most others, including solitary species, are active for shorter periods that are, at least sometimes, linked to the availability of preferred resources (Lindsey, 1958; Minckley et al. 1994; Leong & Thorp, 1999).

While most bee species nest in the ground (Michener, 2007; Spivak et al. 2010; Packer 2010), most of the rest nest in cavities above ground (e.g. pithy or hollowed out plant stems, beetle-bored holes in wood) (Stephen & Osgood, 1965; Krombein, 1967; Bohart, 1972; Grixti & Packer, 2006; Williams et al. 2010). Many cavity-nesting species readily accept artificial nesting habitats in the form of drill holes in wood, or tubes made of glass, plastic, paper or cardboard (hereafter referred to as nest boxes). Nest boxes are unique sampling tools widely used to survey cavity-nesting bees, wasps, and their parasites in many different habitats (Tscharntke et al. 1998; Westphal et al. 2008; Praz et al. 2008; Zurbuchen et al. 2010; MacIvor & Packer, 2015). Nest boxes are also simple to construct, lightweight and inexpensive, and can be readily deployed in large numbers.

Nest provisioning bee and wasp species that use nest boxes construct brood cells in a linear series from the back of the nest to the front, with one egg per cell (Krombein, 1967; Strickler et al. 1996; MacIvor et al. 2014). Brood cells are made of different natural materials depending on the species and each contains sufficient pollen and nectar to provision the

individual larva to adulthood. With some exceptions (e.g. Mason bees: *Osmia* spp.), most larvae spend the winter as pupae, then in spring, develop into adults over a period of time that is coordinated with the availability of their resources (Owen & McCorquodale, 1994).

Soon after emergence, bees and wasps find suitable nesting locations and the availability of nest sites limits their abundance and could influence species composition in an area (Potts et al. 2005; Sardiñas & Kremen, 2014). Since locating large numbers of natural nesting sites can be difficult (Scott, 1993; Hurst et al. 1997), artificial nest boxes for cavity-nesting species are useful proxies in their investigation (Tscharntke et al. 1998; MacIvor & Packer, 2015). Many studies have found that collecting cavity-nesting bees and wasps in nest boxes and rearing them to adulthood provides a useful model for investigating overwintering and reproductive success in response to environmental changes (Tepedino & Parker, 1986; Richards et al. 1987; Yocum et al. 2005; Sheffield et al. 2008a; O'Neill et al. 2011; Fliszkiewicz et al. 2012; Fründ et al. 2013). From nest boxes, identification of larvae to species is challenging and without DNA barcoding (Sheffield et al. 2009), this level of taxonomic resolution requires rearing them to adulthood.

Quantifying incubation periods and time to emergence among hymenopteran species within a community can improve interpretation of synchrony among plant-pollinator and predator-prey interactions (Fitter & Fitter, 2002; Bartomeus et al. 2011; Rafferty & Ives, 2013; Kudo & Ida, 2013; Burkle et al. 2013). This is important for solitary bees that use nest boxes and are being considered for management as alternative pollinators (e.g. non-honey bees) for cultivated crops (Bohart, 1972; Bosch & Kemp, 2002; Sheffield et al. 2008a; Lee-Mäder et al. 2010). Being able to anticipate change within a community of bees can help with planning for artificial nest deployment to support species of concern, the addition of foraging plants (Sheffield et al. 2008b), or acceleration of the release of bees reared *en masse* to synchronize with target crops (Bosch & Blas, 1994; Bosch et al. 2000; Gruber et al. 2011).

While there is considerable information available on incubation and emergence timing of species considered as manageable alternative pollinators, for example, those in the genus *Osmia* and *Megachile* (e.g. Kemp et al. 2004; Kraemer & Favi, 2010), there are relatively few data on emergence timing of most other cavity-nesting bees and wasps (Forrest & Thomson, 2011; Fründ et al. 2013). In this study we examine temporal niche partitioning of 47 co-occurring species of bee, wasp, and parasite species that seek the same nesting habitat by comparing interspecific incubation period and emergence timing. The primary objective was to map seasonality of the regional cavity-nesting bee, wasp, and parasite community to inform enhancement strategies intended to support these taxa including nest box design and management (MacIvor & Packer, 2015) and gardening (Garbuzov & Ratnieks, 2014; Salisbury et al. 2015).

Additionally, we evaluate two hypotheses based on the community of bees, wasps, and parasites using nest boxes. First, although no intraspecific effect of body size on emergence time was recorded in *Osmia cornuta* Latrielle (Bosch & Kemp, 2002) or *Megachile rotundata* Fabricius (Owen & McCorquodale, 1994), interspecific body size in insects has been shown to be positively correlated with development time (Roff, 1992; Blanckenhorn, 2000; Garcia-Barros, 2000), and so we predict that species larger in body size would emerge significantly later. Our second hypothesis has to do with the geographic origin of the nest box colonizer. Since introduced bees usually exhibit variation in traits that allow them to colonize new environments, leading to increased niche overlap with native species (Barthell et al. 1998; Goulson, 2003), we hypothesize that introduced species would have greater variation in emergence timing compared to native species. To test these hypotheses we compare emergence time between all species as well as between phylogenetically independent contrasting pairs of species, in order to control for evolutionary relationships in emergence time (Felsenstein, 1985; Garland et al. 1992).

3.3 Methods

The specimens used for this study were obtained from a sample of 200 nest boxes set up each year from May to October for three years (2011-2013) as described in Chapter 1. In October, nest boxes were collected, each cardboard tube opened and the brood cells removed. The contents of each brood cell were labeled with a unique identifier and placed into individual cells within 24-cell assay trays with the lid on. A complete incubation process includes a sufficiently long cooling period (Bosch & Kemp, 2004) so all specimens spent the cold season (October – March) in a walk-in fridge kept at a constant 4°C (as in Bosch et al. 2000).

Each year in late-March the assay trays containing all brood cells from the previous year were moved from the walk-in fridge and into a sealed growth chamber where temperature and humidity were maintained at 26°C and 60%, respectively (Johansen & Eves, 1973; Tepedino & Parker, 1986). All species overwintered as larvae except for mason bees (*Osmia* spp.), and a parasite, *Sapyga centrata* [that attacks *O. pumila* (Goodell, 2003)] that overwintered as adults. The growth chamber was windowless and kept dark for the duration of the study except when lights were turned on during daily inspection of brood cells to measure emergence timing (as in Sheffield et al. 2008a). Approximately 3% of all cells in the growth chamber were lost to parasitic *Melittobia* and *Monodontomerus* wasps that emerged early and attacked other larvae still undergoing development. To reduce their depredations, four traps, each consisting of a black light and a bowl filled with water and dish soap, were set up to attract and reduce the number of these minute wasps that emerged and escaped the assay tray (Eves et al. 1980). For each individual, day of emergence was recorded as the number of days from the beginning of incubation to the time of development to adulthood (Owen & McCorquodale, 1994; Sheffield et al. 2008a).

3.3.1 Analysis

To determine whether there was a significant difference in emergence timing among all species, an analysis of variance (α=0.05) using SPSS v22 was completed. This was followed by a Tukey *post hoc* analysis to examine whether there were significant differences among species of bee, wasp, and parasite. A Pearson's R correlation was used to examine whether the variation in emergence time, as determined by the standard error of the mean, increased with increasing mean emergence time by species.

To examine the effect of body size we measured the distance between wing bases, or the intertegular (IT) span (Cane, 1987; Greenleaf et al. 2007; Williams et al. 2010) on a sample of 5–10 individuals per species. Measurements were made using an ocular micrometer attached to a dissecting microscope. First, a linear regression was used to compare interspecific body size and mean emergence time among all species investigated. Second, to control for any effects of phylogeny (Garland et al. 1992), we paired congeneric species that differed in body size and grouped either as "large" or "small" to test for significant difference using a paired t-test (α=0.05). Phylogenetically independent pairs of congeneric species were selected from the pool of species by constructing a phylogeny in TNT (Goloboff et al. 2008) based on a character matrix developed from existing phylogenies [*Megachile*; Gonzalez (2008), *Hylaeus*; Kayaalp et al. (2013), Vespids; Carpenter (2003)]. Pairs were made between a species and its closest relative within the same genus where possible. Finally, a paired t-test was used to compare time to emergence between native and exotic colonizers (as determined by Giles & Ascher, 2006; Ascher & Pickering, 2015; Packer et al. 2015), again based on phylogenetically independent 'native - exotic' species pairs.

3.4 Results

After three years of sampling a total of 84 species of bee, wasp, and parasite were identified (MacIvor & Packer, 2015). Rearing individuals to adulthood, the number of days to emergence time was recorded for 47 species and 8,006 individuals (Figure 10). Species that consisted of less than 5 individuals that emerged over all study sites and years were not included in the analyses due to low sample size. Of the 47 species examined, there were 22 species and six genera of bee in two families (all in the superfamily Apoidea) (*Hylaeus* – Colletidae, and *Osmia, Heriades, Hoplitis, Chelostoma, Megachile* – all Megachilidae) and 16 species of nest provisioning wasp in nine genera, four families and two superfamilies (*Isodontia* – Sphecidae; *Passaloecus, Psenulus, Trypoxylon* – Crabronidae (both families belong to the Apoidea – these are the apoid wasps)*; Ancistrocerus, Euodynerus, Symmorphus* – Vespidae; and *Auplopus, Dipogon* – Pompilidae (both these families belong to the Vespoidea)) (Figure 10). Nine species in seven genera and 5 families of parasite were identified from emerged individuals from three orders (Hymenoptera, Coleoptera, Diptera), and two parasites, *Ephialtes manifestator* (Linnaeus) and *Anthrax irroratus* Say had more than one host (Table 4).

Among all species, mean day of emergence (e.g. number of incubation days to emergence of adult) was significantly different (F_{47}=786.29, $p<0.001$) and ranged from 0 to 38 (Figure 10). Many significant differences were noted among species, including one that was expected: Mason bees (*Osmia* spp.) emerged significantly earlier than all others because they overwinter as adults (Fye, 1965; Bosch et al. 2001) (Figure 10). The aptly named, large resin bee, *Megachile sculpturalis* was the largest species recorded in our study and emerged significantly later than all other species (average duration to emergence=37.4±0.7 days; mean±SD) (Figure 10). The greatest overlap (i.e. times to emergence did not differ significantly) occurred between day 12 and 17, when 15 species (10 nest provisioning wasps, 3 bees, and 2 parasites) emerged (Figure 10).

Differences between the mean day of emergence of parasite and host varied depending on the type of parasite. For example, the brood parasite *A. irroratus* emerged 25 days after its host whereas emergence of three cuckoo parasites were more similar to that of their hosts: *Chrysis cembricola* Krombein emerged on the same day as *Symmorphus canadensis* (de Saussure), *Caenochrysis doriae* (Gribodo) emerged an average of 2.8 days later than its host *Trypoxylon frigidum* Smith, and *Caenochrysis tridens* (Lepeletier) emerged on average 7.7 days earlier than its host *Trypoxylon collinum* Smith (Figure 10). No difference in emergence timing between phylogenetically independent pairs of native and introduced species was evident (t_8= -1.769, p = 0.115) [(native - introduced): *Ancistrocerus adiabatus* (Saussure) - *Ancistrocerus antilope* (Panzer), *Passaloecus cuspidatus* Smith - *Passaloecus gracilis* (Curtis), *Trypoxylon frigidum* Smith - *Psenulus pallipes* (Panzer), *Heriades carinata* Cresson - *Chelostoma rapunculi* (Lepeletier), *Hylaeus affinis* (Smith) - *Hylaeus hyalinatus* Smith, *Megachile relativa* Cresson - *Megachile centuncularis* (Linnaeus), *Megachile campanulae* (Robertson) - *Megachile rotundata* (Fabricius), *Megachile pugnata* Say - *Megachile sculpturalis* Smith, *Osmia pumila* Cresson - *Osmia caerulescens* (Linnaeus)].

A Pearson's R correlation showed there was no significant difference in variance in emergence time among species with developmental mean day to emergence (Figure 11). Variance in the time to emergence was greatest in species emerging during the middle of the incubation period. The time to emergence was positively correlated with body size when all 47 species were included in a linear regression analysis (Figure 12). The mean day of emergence also increased significantly between large and small-bodied species when analyzed using phylogenetically independent contrasting pairs (Figure 13).

4.5 Discussion

From the entire sample, we found that the mean day of emergence of cavity-nesting bees, wasps, and parasites was highly conserved within species, but that there were many significant differences among species (Figure 10). Emergence timing might further vary under natural conditions because of environmental variation (Forrest & Thomson, 2011). We incubated bees in a controlled growth chamber, however our data show a strong temporal partitioning of niche among species sharing similar nesting conditions (Budrienė et al. 2004).

Increasing body size was significantly correlated with longer times to emergence between species (Figure 12), Controlling for phylogeny, congeneric pairs of small and large species also showed that the latter had significantly longer mean emergence times (Figure 13). Despite controlled post-winter warming conditions, our first hypothesis that larger species would emerge later than smaller species was supported. Our findings agree with other comparative studies that show larger insects take longer to develop. Being larger can confer a number of benefits; for example, larger bee species can collect more pollen on their body (e.g. Kendall & Soloman, 1973) and larger wasps can carry larger prey (e.g. O'Neill, 1985; Coelho, 1997). However, longer periods of time as pupae in a nest could increase mortality by parasitism or predation (Stearns & Koella, 1986; Blanckenhorn, 2000). These kinds of data can inform our understanding of the impacts of interspecific differences in body size among insects, which can influence the structure and composition of a community (Chown & Gaston, 2010). These details can also inform enhancement strategies that target species or communities that provide important ecological services. For example, replacement of nesting tubes of the same widths as they are completed with fresh unused ones to alleviate competition for nesting resources between and among species of similar body sizes over time (Bohart, 1955; Sheffield et al. 2008a; Delphia & O'Neill, 2012).

Our second hypothesis: that introduced species would have greater variation in emergence timing compared to native species was rejected as no difference between these groups was observed when phylogenetically independent contrast approaches were incorporated. Other studies have found introduced species to be successful in new environments because they exhibit traits that permit variability in resource use and adaptation to novel conditions (Richard & Hamilton, 1997; Henle, 2004; Sol & Lefebvre, 2000; Da Mata et al. 2010). Our study suggests variability in emergence time is not a trait that varies among introduced and native species. Rather, more work is needed to determine how variation in other traits might enhance invasive competitiveness. Examples might be aggressiveness, flexibility in nesting material preference, or rates of foraging efficiency (Barthell et al. 1998; MacIvor & Salehi, 2014).

Species with a later mean day of emergence did not exhibit greater variation in emergence time than early emerging species. Bees in the genus *Osmia* and one specialist parasite of *O. pumila*, the wasp *Sapyga centrata*, emerged significantly earlier than all other species, with little variation in mean day of emergence (Figure 10). On the other hand, the introduced *Megachile sculpturalis*, the largest species in the study, had the longest emergence time, presumably because it is tropical in origin (Mangum & Sumner, 2003). Since its nests are constructed using tree resins they are similar in appearance but larger than those of *M. campanulae* a native resin bee that emerges significantly earlier (day=27.2±3.3). Finding out the duration of nesting in both species and removing nest tubes of a suitable size after the native species has finished could be important for the local removal of the introduced species to ensure it does not compete with native species for nesting habitat (Roulston & Malfi, 2012).

Between day 12 and 17 there was an overlap in the mean day of emergence among ten nest-provisioning wasp species (Figure 10). These wasp species are each predators of a number of different spiders (Medler, 1967), caterpillars (Cowan, 1981), or aphids (Fricke, 1993).

Since many of these wasps were of similar size, nesting habitats could be a more limiting interspecific resource than prey (Wcislo, 1996; Potts et al. 2005). Understanding the relationship between foraging and nesting resources could help practitioners estimate the number of available nesting tubes in nest boxes needed to enhance the management of arthropods with cavity-nesting wasps (Harris, 1994), as well as pollination by bees.

Interpreting parasite type, diversity and host associations can inform interpretations of parasites as indicators of habitat quality and community level change (Wcislo, 1987; Horowitz & Wilcox, 2005; Sheffield et al. 2013). Some authors have noted that parasitoids are synchronized with hosts such that they emerge later relative to them (Thorp et al. 1983; Baker et al. 1985). These parasites are typically those that attack larvae and so emerging after the host ensures that prey will be available. Assuming parasites live as long as their hosts, their emerging soon after the host will ensure that all host offspring are available for attack. For example, in our study the parasitoid *Anthrax irroratus* attacked two *Osmia* species and emerged 25 days after both hosts (Table 4). Scott & Strickler (1992) also recorded *A. irroratus* emerging one month after its hosts, *Megachile relativa* and *M. inermis* Provancher*,* which were not attacked in our study presumably because of low numbers of colonizers. The fly larvae develops on the prepupae of the host after hatching from a tiny egg 'flicked' indiscriminately into the nest by the fly as she hovers in front of the nest entrance (Minckley, 1989). The larvae overwinter and develop to adults in the spring (Gerling & Hermann, 1976). Cleptoparasites on the other hand replace the host egg with their own, or their early instar larvae kill the host egg or larva, and so emerge at a more similar time (Forrest & Thomson, 2011). In our study, cleptoparasites included *Chrysis cembricola*, *Caenochrysis doriae* and *Caenochrysis tridens,* which all emerged within a week of their hosts (Figure 10).

Documenting the identity and emergence times of co-occurring solitary bees, wasps, and parasites can provide significant information about competition and niche overlap in these

important taxa (Frankie et al. 1998; Tscharntke et al. 1998; Bosch & Kemp, 2002; Tylianakis et al. 2007; Forrest & Thomson, 2011). Cavity-nesting bees and wasps that share a common nesting resource, readily accept artificial nest boxes, and are easily managed, are excellent model organisms for these investigations. In our study of 47 species of bee, wasp, and parasite, we find that intraspecific emergence timing was conserved whereas interspecific timing was highly significantly different. There was no difference in emergence time between native and introduced species, but larger species emerged significantly later when phylogenetic effects were controlled for. Interpreting emergence timing and overlap in the use of nest boxes can improve management of target bee and wasp species by for example, knowing when to replace nest tubes with fresh empty ones (e.g. post emergence of *Osmia*) or predict timing of undesirable species requiring control (e.g. removal of *M. sculpturalis*).

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3.7 Table

Table 4. Parasite-host associations determined post-emergence as recorded from nest boxes in the study region over the three years of sampling. ‘Days’ represent the difference in mean day of emergence between the parasite and the host. For parasites having more than one host, ‘Days’ was calculated for each parasite-host pair.

Parasite	**Family**	**Order**	**Days**	**Hosts**
Sapyga louisi Krombein	Sapygidae	Hymenoptera	+ 7.7	*Heriades carinata*
Sapyga centrata Say	Sapygidae	Hymenoptera	+ 0.1	*Osmia pumila*
Ephialtes manifestator (Linnaeus)	Ichneumonidae	Hymenoptera	- 2.7	*Passaloecus gracilis,*
			+ 3.1	*Passaloecus cuspidatus,*
			- 1.7	*Trypoxylon frigidum*
Perithous divinator (Rossi)	Ichneumonidae	Hymenoptera	*- 3.6*	*Psenulus pallipes*
Chrysis cembricola Krombein	Chrysididae	Hymenoptera	*- 0.6*	*Symmorphus canadensis*
Caenochrysis doriae (Gribodo)	Chrysididae	Hymenoptera	*+ 2.8*	*Trypoxylon frigidum*
Caenochrysis tridens (Lepeletier)	Chrysididae	Hymenoptera	*- 7.7*	*Trypoxylon collinum*
Nemognatha piazata (Fabricius)	Meloidae	Coleoptera	*- 4.3*	*Megachile rotundata*
Anthrax irroratus Say	Bombyliidae	Diptera	*+ 24.2*	*Osmia caerulescens,*
			+ 24.3	*Osmia pumila*

3.8 Figures

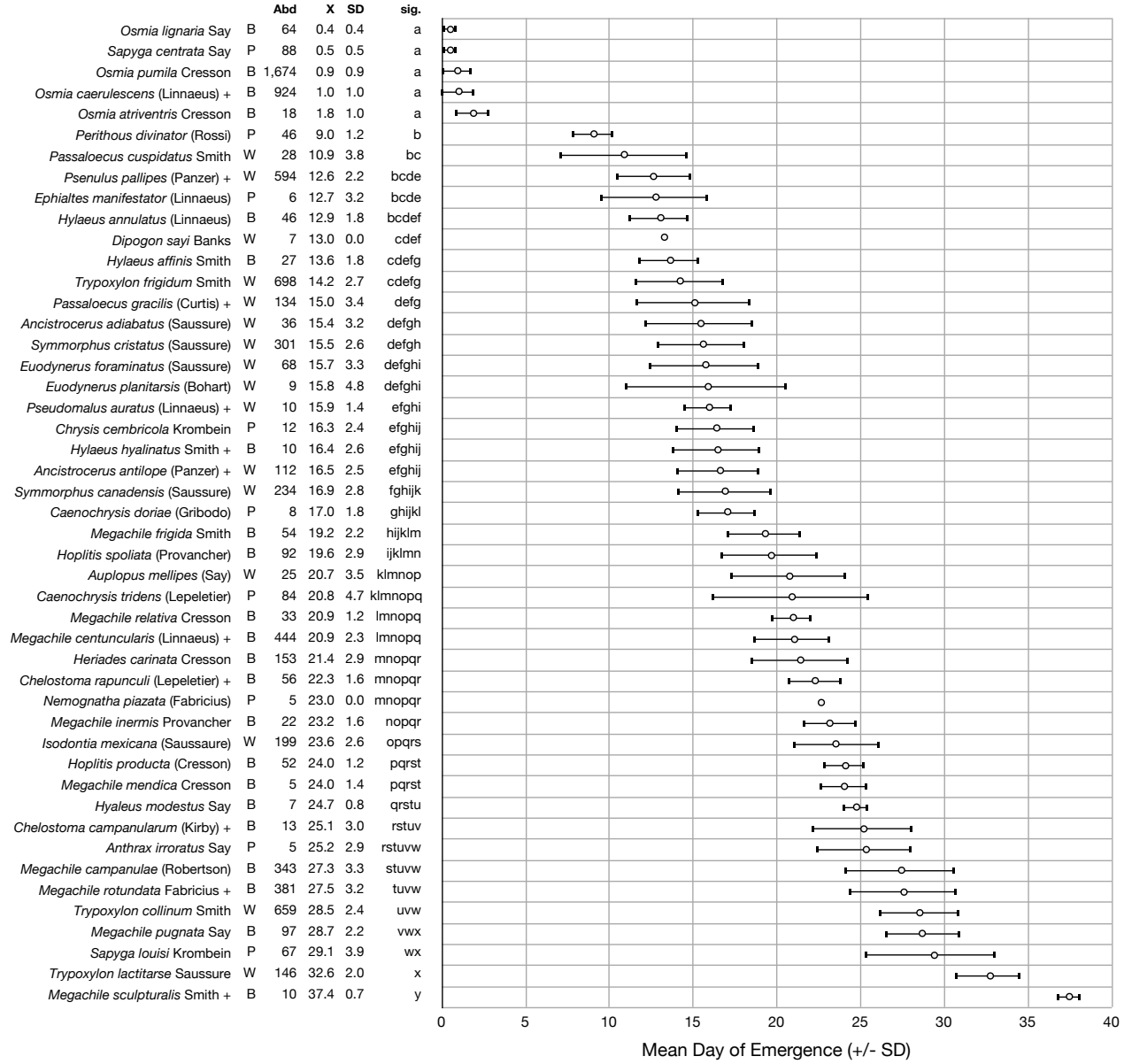

Figure 10. Variation in the mean day of emergence of species of bee, wasp, and parasite recorded from individuals taken from nest boxes. 'Taxa' denotes bees (B), nest provisioning wasps (W), and parasites (P). 'Abd' is the total number of individuals incubated and emerged successfully. 'X' is the average number of days taken to emerge and 'SD' is the standard deviation of the mean. Significant differences between species 'sig' were given alphabetically where species sharing a letter were not significantly different from one another ($\alpha = 0.05$). Those species denoted with a "+" are considered introduced to the region.

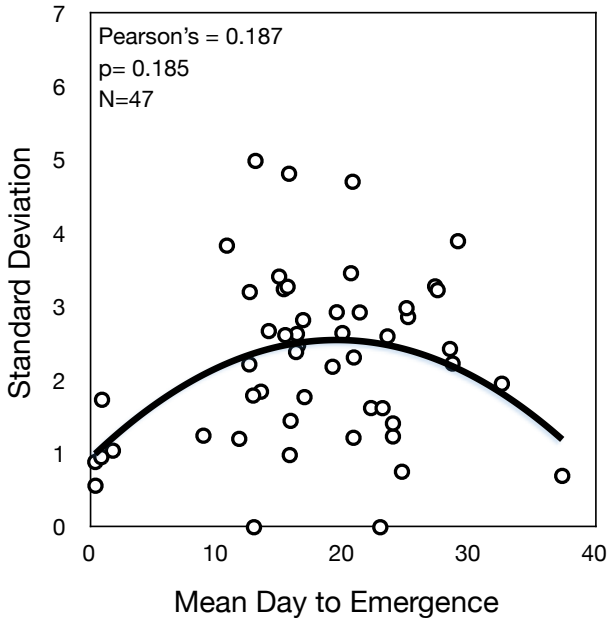

Figure 11. Scatterplot correlating mean emergence time and the standard deviation to examine variation between early and late emerging species. No correlation was detected but more variation was evident among mid-season emerging species.

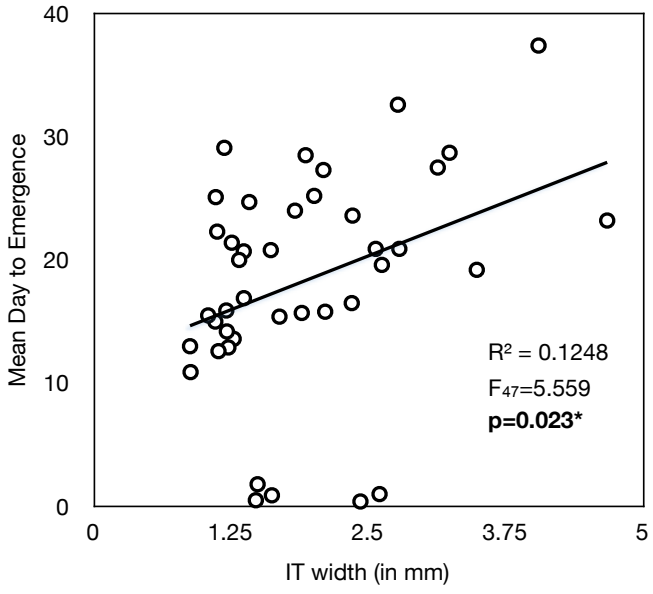

Figure 12. Scatterplot showing correlation between time to emergence and body size as measured by the intertegular width

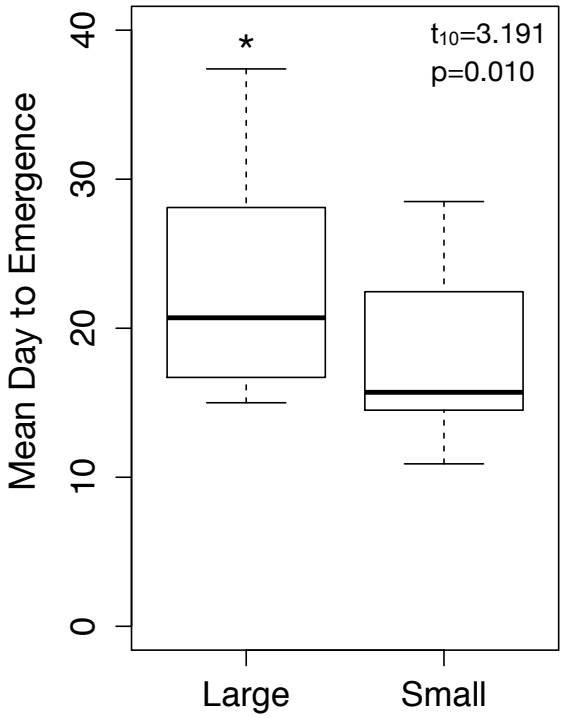

Figure 13. A boxplot showing difference in mean time to emergence between large and small phylogenetically independent congeneric pairs of species. Pairs included: *Auplopus mellipes - Dipogon sayi, Trypoxylon lactitarse - Trypoxylon collinum, Passaloecus gracilis - Psenulus pallipes, Ancistrocerus antilope - Ancistrocerus adiabatus, Euodynerus foraminatus - Euodynerus planitarsis, Symmorphus canadensis - Symmorphus cristatus, Hylaeus modestus - Hylaeus affinis, Osmia caerulescens - Osmia pumila, Chelostoma campanularum - Chelostoma rapunculi, Hoplitis spoliata - Hoplitis producta, Megachile sculpturalis - Megachile campanulae, Megachile pugnata - Megachile centuncularis, Megachile rotundata - Megachile relativa.*

Chapter 4: The bees among us: Modelling occupancy of solitary bees in urban landscapes

4.1 Abstract

Occupancy modelling has received increasing attention as a tool for interpreting the probability of a species being present at a site whether or not it was detected in sampling. It is thought to be particularly useful when a species of interest is spread out over a large area and sampling is constrained. We used occupancy modelling to estimate the probability of three introduced [*Megachile rotundata* Fabricius*, Megachile centuncularis* (Linnaeus)*, Osmia caerulescens* Linnaeus], and three native solitary bees [*Megachile campanulae* (Robertson)*, Megachile pugnata* Say*, Osmia pumila* Cresson] (Apoidea: Megachilidae) being present when repeated sampling did not find them. Our study occurred along a gradient of urbanization and uses nest boxes (bee hotels) set up over three consecutive years. Occupancy modelling produced different conclusions as to where species are compared to that indicated by species detection and abundance-based data alone. For example, it predicted that the species that was ranked 4th in terms of detection actually had the greatest occupancy estimate among our species. Introduced *M. rotundata* and *M. centuncularis*, and one native (*M. campanulae*) had modelled occupancy values that increased with increasing urbanization. The native *M. pugnata* had decreased occupancy with increasing building footprint, whereas the same pattern was found for *O. pumila* only in sites containing >40% building footprint. A combination of occupancy modelling and abundance-based sampling is the best way to ensure wildlife management is effective and targets the right habitat.

4.2 Introduction

A persistent problem with biodiversity surveys is that of false absence: when a species is present at the site but not detected in a sample (MacKenzie et al. 2002). This limitation is only readily assessed with repeated sampling at multiple locations or times where non-detections are interspersed among instances of detection. Interpreting non-detection as absence will underestimate a species' temporal and/or spatial distribution (Bailey et al. 2004; MacKenzie et al. 2006). This can decrease the accuracy of habitat models (MacKenzie & Royle, 2005) and may weaken the accuracy of wildlife management recommendations (Tyre et al. 2003; Bailey et al. 2004; Field et al. 2005; Lobo et al. 2010; Tanadini & Schmidt, 2011; Welsh et al. 2013). The probability of detecting a species is related to species occupancy (Ψ), a state variable that estimates the proportion of sites that are occupied by a species, whether or not it was detected in surveying (MacKenzie et al. 2002). Occupancy, as estimated with Ψ, does not consider abundance, only the presence or absence of a species at a site during sampling (Polluck et al. 2002; Guillera-Arroita et al. 2010; Olea & Mateo-Tomás, 2011). Patterns in detection and non-detection allows for estimation of a species' detection probability (p), and the proportion of non-detection that actually indicates true absences (MacKenzie et al. 2002).

Occupancy models incorporate both Ψ and p and are especially useful for interpreting survey data for species that are difficult to sample, and/or where populations are common and/or widespread but extensive sampling is prohibitive in either cost or time (MacKenzie et al. 2006). These models can be used to assess suitability among sites where the species of interest was not detected (Gu & Swihart, 2004; MacKenzie et al. 2009). In sum, occupancy modelling should provide a more reliable picture of when and where a species might actually be in a series of samples whether the species was found in all sampling events or not (Hanski, 1994; Bradford et al. 2003; Bailey et al. 2004; Kawanishi & Sunquist, 2004; Studds & Marra, 2005; MacKenzie et al. 2009; Guillera-Arroita et al. 2014).

Here we present the results of occupancy modelling on six bee species, three native and three introduced, in a large urban landscape and demonstrate that conclusions based on sampled detection alone are often different from those based upon occupancy. Welsh et al. (2013) argued that results from occupancy models can be highly variable depending on the number of individuals surveyed and that interpreting them can be as misleading as ignoring non-detection in abundance-based studies. However here we find occupancy models provide additional insights into differences between introduced and native bee species: native bees are demonstrated to be more widespread than introduced bees in cities than their sampled locations suggest. Our data support the notion that occupancy modelling produces more meaningful results by partitioning true absence from false non-detection. Occupancy modelling should become routine in biodiversity survey work, especially in situations where false non-detection might mislead management decisions.

4.2.1 Bees

Bees are essential pollinators in most terrestrial landscapes for both agricultural crops (Klein et al. 2007; Kennedy et al. 2013; Klatt et al. 2014) and wild plants (Ollerton et al. 2011). Consequently, they have been studied using a variety of abundance-based sampling techniques (e.g. Frankie et al. 1998; Williams et al. 2001; Grixti & Packer, 2006; Westphal et al. 2008; Leonhardt et al. 2013). Discovery of bee declines has resulted in increased monitoring, conservation action, and public awareness (Kearns et al. 1998; Biesmeijer et al. 2006; Colla & Packer, 2008; Osborne et al. 2008; Byrne & Fitzpatrick, 2009; Williams et al. 2010; Garbuzov & Ratnieks, 2014; Kerr et al. 2015).

Irrespective of sample size, bee surveys often contain many species represented as singletons (Oertli et al. 2005; Sheffield et al. 2013) and it is difficult to measure species diversity accurately when many are rare (Williams et al. 2001). Also, as bees forage away from their nest

(Gathmann & Tscharntke, 2002; Greenleaf et al. 2007; Zurbuchen et al. 2010), their presence in samples may not be indicative of habitat suitability at the sample site per se. For example, individual bees may be just 'passing through' the habitat or sample site under investigation (Grixti & Packer, 2006).

Suitable foraging habitat for bees in urban landscapes is fragmented and heterogeneous, consisting of a mix of small and large patches supporting a diverse array of flowering plant species and horticultural varieties (Gibb & Hochuli, 2002; Cane et al. 2006; Matteson & Langellotto, 2010). Perhaps unsurprisingly, bee diversity declines with increasing urbanization (McFredrick & LeBuhn, 2006; Hernandez et al. 2009). However, one functional group, the cavity-nesting bees, appears to be less affected by urbanization (Cane et al. 2006; Matteson et al. 2008). This is presumably because suitable nest sites are more numerous due to increased numbers of cut plant stems, urban infrastructure (e.g. holes in building materials) (Cane et al. 2006), and nest boxes (see Lee-Mäder et al. 2010). Nest boxes are inexpensive to build and easy to monitor (MacIvor & Packer, 2015). As they sample bee broods directly, nest boxes can be used to assess habitat quality because they do not include taxa that are merely passing through the area (Tscharntke et al. 1998).

In this study we use occupancy modelling to investigate differences in populations of native and introduced cavity-nesting bees in nest boxes at sites >250m apart throughout a large urban landscape over three years. We compare results among introduced and native species because introduced bees can have negative impacts on both native bees (Goulson, 2003; Madjidian et al. 2008; Hudewenz & Klein, 2013; Morales et al. 2013) and pollination networks (Aizen et al. 2008). Introduced bees are increasingly represented in surveys of wild bees (Barthell et al. 1998; Grixti & Packer, 2006; Matteson, Ascher & Langellotto, 2008; Gardiner et al. 2009; Bartomeus et al. 2013; MacIvor et al. 2014). Moreover, because bees that are introduced from one continent to another are moved by human activity, a greater level of

synanthropic adaptation might be found among them (Lizée et al. 2011). Consequently, our first hypothesis is that introduced species would have greater occupancy probabilities than native species. Changes in species diversity patterns in urban landscapes have been linked to the presence of infrastructure such as the proportion of an area occupied by buildings (Godefroid & Koedam, 2007; Matteson & Langellotto, 2010). Thus, our second hypothesis was that occupancy probability for all bees examined would decline along a gradient of increasing urbanization as determined by the proportion of building footprint surrounding a site.

4.3 Methods

4.3.1 Sampling

Nest boxes were set up at each of 200 sites throughout the city of Toronto and the surrounding region each year from 2011-2013 as described in Chapter 1. They were retrieved from 149 sites in all three sampling years. For occupancy modelling, Tyre et al. (2003) found a minimum of three repeated visits was sufficient to eliminate biases associated with false absences. As nest boxes provide data on annual detection, our three years of sampling allowed us to interpret spatial occupancy patterns not apparent from detection or abundance data alone (MacKenzie et al. 2002). Four urban green space types ("type") were differentiated: residential gardens, community gardens, urban parks, and building rooftops. Residential gardens were either front- or backyards occurring on privately owned property and maintained by a homeowner. Community gardens occupied a central location: e.g. in a neighbourhood park, the grounds of an apartment complex, or in a hydro corridor, where groups of people garden collectively. Urban parks were sites contained within the boundaries of named parks as designated by the City of Toronto and the Toronto and Region Conservation Authority (TRCA). These are usually grassy areas with sparse tree cover but usually with planted flowerbeds around the edges or along paths (Gilbert, 1989). Building rooftop sites were atop single buildings upon which vegetation

(e.g. planters, green roofs) had been installed. Green roofs are increasingly common in Toronto where they are mandatory on new buildings of certain types (Torrance et al. 2013).

From the nest box sample, a total of 36 bee species were found, and six megachilids were selected for occupancy modelling because they were common and widespread (MacKenzie et al. 2006) (Table 5). Since the differences in response to urbanization between native and introduced bees might be phylogenetically constrained, we grouped the native and introduced bees (Cane, 2003; Giles & Ascher, 2006) into pairs that exhibit reciprocal monophyly. Based upon available phylogenies (Gonzalez, 2008), the species pairs are as follows (native species first within each pair): *Osmia pumila* Cresson + *O. caerulescens* L.; *Megachile campanulae* (Robertson) + *M. rotundata* (Fab.); *M. pugnata* Say + *M. centuncularis* (L.).

4.3.2 Analysis

City of Toronto RMSI (Resource Management Strategies Inc.) municipal spatial reference data shapefiles (York University Map Library, Toronto, Ontario) were examined using geospatial tools in ArcGIS v.10 (ESRI, Toronto, Canada). To determine site variables potentially impacting bee presence, the building footprint (m^2 - 'foot') within a 600m radius was determined for each nest box, which is within commonly found maximum foraging ranges of solitary bees (Greenleaf et al. 2007; Zurbuchen et al. 2010). Building footprints were summed for all building types because they were applicable citywide across different land use types (Davies et al. 2008). This metric was extracted using the buffer and clip tools in ArcGIS within a 200m radius surrounding each site. Z-scores were calculated to standardize the building footprint values prior to statistical testing.

Presence/absence data for the six bee species were recorded from nest boxes at each site for each year and analyzed using PRESENCE (MacKenzie et al. 2006). This program permits the user to estimate the proportion of sites occupied (Ψ) and the detection probability

per site (*p*) for specific taxa in relation to different site variables. To interpret Ψ from each site over the three years, each year was considered a single sample. Multiple-season models using PRESENCE require multiple samples for each season whereas we had one sample for each of three years. Consequently, data were collapsed into the single-season feature in PRESENCE, which is conventionally used to fit multiple samples from a single season (MacKenzie et al. 2006).

Model equations were fitted to Ψ and *p* parameters for each species and were permitted to vary with the site variables in every combination holding neither, both or one of occupancy and detection probabilities constant. They were each bootstrapped 1000 times. The model of best fit (Table 5) was determined using AIC model selection (Burnham & Anderson, 2004) for each species (Appendix I).

A non-parametric Spearman's rho correlation test was used to determine whether Ψ estimates were correlated with the following state variables: species detection, total species abundance and number of nesting tubes colonized recorded over all sampling sites/years. This was examined first using Ψ estimates for each species from their individual model equation of best fit (Table 5) then repeated, each time using the best model equation for all six species combined (results given in Appendix I). Linear regression analysis ($\alpha=0.05$) was used to compare individual species Ψ estimates against building footprint and the coefficients qualitatively compared among the six species. Further, for each species, an independent t-test was used to compare occupancy probabilities from sites with less (N=133) or more (N=16) than 40% building footprint. This cut-off was used to indicate change to a dense urban core [50% was used by Fortel et al. (2014), but this would have provided us with too few high density sample sites]. Finally, for each species, an analysis of variance (ANOVA) examined the difference in occupancy probabilities among the four urban green space types defined. All analyses in the study except those using PRESENCE were completed using the R Studio statistical program

v0.98 (R Core Team, 2014).

4.4 Results

Among the six bee species examined, the ordering of species by predicted occupancy (Ψ) different from that based upon actual detection, total abundance, or the number of nesting tubes colonized (Figure 15; Appendix J). Introduced *O. caerulescens* and *M. rotundata* and the native *O. pumila* were all present at more sites and were more abundant than *M. campanulae* (Figure 15A), even though the Ψ for the latter species was significantly greater than that of each of the other species, except *O. pumila* (Figure 16). Variance in Ψ was also less among our three introduced species than for the native ones. Higher variance in Ψ suggests that to better characterize native species more sampling effort is required (MacKenzie & Royle, 2005).

The model equations of best fit for interpreting data as determined by AIC selection are shown in Table 5. They were the same for the native bees *M. campanulae* and *O. pumila* model= Ψ(site),*p*(.) (Table 5). For two introduced bees, *M. rotundata* and *O. caerulescens*, the best fit was obtained with: model=Ψ(site),*p*(foot,site) (Table 5). Data for introduced *M. centuncularis* were best described by a third model equation: model= Ψ(foot),*p*(.), and the native *M. pugnata* data were best fit with a fourth: model=Ψ(foot,site),*p*(site). Species abundance was not significantly correlated with Ψ estimates using the models of best fit for all species or for any of the other top model equations with less optimal AIC values (Appendix J).

The model equations of best fit indicated that only *M. pugnata* was negatively affected by the proportion of building footprint surrounding the nesting site within a 600m radius (Figure 17). However, when Ψ values for each species were split between sites with more or less than 40% building footprint, another native, *O. pumila* also exhibited significantly lower occupancy estimates at high building density (>40% Ψ=0.458, <40% Ψ=0.648; df=149, t=10.643, p<0.001).

The type of urban green space had a significant impact on Ψ of two native species, *M.*

campanulae and *O. pumila*, and one introduced bee *O. caerulescens* (Figure 18). Both native species had Ψ greatest in residential gardens while *O. caerulescens* had significantly greater Ψ in community gardens compared to roofs, but not when compared to parks or residential gardens (Figure 18). Differences in Ψ among site types for introduced *M. rotundata* approached significance, with residential gardens exhibiting the greatest estimates.

4.5 Discussion

This study is the first to employ occupancy modelling as a tool to estimate patterns in bee species non-detection where absence was not certain. We found that occupancy probabilities provided additional details for each species that were not evident from interpretation of detection or abundance data alone (Figure 15). For example, *M. campanulae* had the greatest Ψ recorded among all six bees, e.g. it was predicted to be present at the most sites whether it was found in the nest boxes or not. However, *M. campanulae* ranked 4th in detection, abundance, and the number of nesting tubes colonized. This illustrates the value in the additional data provided through occupancy modelling: even though *M. campanulae* was less abundant overall, interpreting non-detection using occupancy modelling predicted it to be the most ubiquitous.

Occupancy probability estimates were more variable among native bees and more consistently high among introduced species (Figure 18). However, there was no indication that introduced bees exhibited significantly higher Ψ than native bees overall, leading to the rejection of the hypothesis that their occupancy would be higher. The native bees, *M. campanulae* and *O. pumila* exhibited the greatest occupancy probabilities among all those tested (Figure 16) despite two introduced species (*M. rotundata* and *O. caerulescens*) having higher site detection and total abundance (Figure 15). This example provides evidence that native bees may occur more broadly in urban environments (Banaszak-Cibicka & Zmihorski, 2012; Fortel et al. 2014) than evident from abundance-based studies that find the most common species to be introduced

ones (Blair, 1996; Suarez et al. 1998; Matteson et al. 2008).

4.5.1. Gradient of urbanization

Overall, increasing urbanization, as determined by surrounding building footprint, was not correlated with Ψ for five of the six bee species. Increased building density had a strong, significantly negative impact on Ψ of the native, *M. pugnata* which declined to 0 occupancy at sites with >30% building footprint (Figure 17). Moreover, although *O. pumila* was the most abundant species and had high Ψ indicating it to be widespread in the urban landscape, its occupancy declined significantly once building footprint was greater than 40%. Based upon our data *in toto*, we accept the second hypothesis that Ψ by native bees would decline significantly more with building footprint than that of introduced bees.

Other studies of urban bee communities find greater bee diversity in areas of low to medium urbanization (Fetridge et al. 2008; Fortel et al. 2014; Baldock et al. 2015) and fewer species in the dense urban core (Hostetler & McIntyre, 2001) where the proportion of impervious surface is highest (McDonnell et al. 1997). However, apart from *M. pugnata*, all other *Megachile* species exhibited a positive correlation between occupancy probability and building footprint. Two of these are introduced species (*M. rotundata, M. centuncularis*).

4.5.2. Urban green space type

Occupancy probabilities for the natives, *M. campanulae* and *O. pumila* were significantly highest in residential gardens compared to our other urban green space types (Figure 18). *Megachile campanulae* uses resins for nesting materials, obtaining them from a variety of plants including pine trees (MacIvor & Salehi, 2014), which are widely planted in residential landscapes and other nearby urban green spaces. *Osmia pumila* also has its nesting material requirements [mud and masticated leaves (Goodell, 2003)] widely distributed among our urban study sites. This

supports the view that residential gardens are suitable for many native bees and may be critical in maintaining bee populations in urban landscapes (Frankie et al. 2009; Lowenstein et al. 2014; Pardee & Philpott, 2014).

Among introduced bees, *O. caerulescens* had Ψ that was significantly higher in community gardens than elsewhere (Figure 18). Not surprisingly, community gardens have also been identified as hotspots for urban bees (Matteson & Langellotto, 2009; Ahrne et al. 2009; Pawelek et al. 2009) as well as pollination services (Potter & LeBuhn, 2015). Occupancy probabilities for the other two introduced bees, *M. centuncularis* and *M. rotundata* did not differ significantly among site types, indicative of their flexibility to persist in a wide variety of urban green spaces (even vegetated rooftops), a feature likely resulting in their success in their introduced ranges (Pitts-Singer & Cane, 2011; Banaszak-Cibicka & Żmihorski, 2012). Although introduced bees can be effective pollinators of cultivated crops (Bohart, 1972; Stephen, 2003; Pitts-Singer & Cane, 2011) they disproportionately visit exotic flowers that could outcompete native plants (Stout et al. 2002; Morales & Aizen, 2002; MacIvor et al. 2014). Occupancy modelling could be used to estimate changes in introduced and native bees that left unchecked could outcompete native bees (Barthell et al. 1998). Our application of occupancy modelling to urban bee populations contributes to the growing body of literature using the technique, which has wide-ranging utility in the study of diverse taxa and environments under management.

4.5.3. Conclusion

This study illustrates the importance of including Ψ as a state variable in biodiversity survey work: it yielded patterns that were significantly different from those based upon detection and abundance data alone. One major finding was that the ranking of occupancy was quite different than that of detection or abundance. We find that using estimates of occupancy probability in conjunction with abundance-based sampling improved the accuracy of predicting bee species

community compositional change in response to environmental conditions, such as variables indicative of the degree of urbanization and site type.

Inclusion of environmental variables in occupancy modelling could improve the precision of resulting estimates and increase the accuracy of monitoring or management of introduced species (Jimenez-Valverde et al. 2011). For example, the combination of nest box sampling with occupancy modelling will allow us to estimate the probability of the species of interest being discovered at other sites. This may be particularly useful for determining probable areas of occupancy of aggressively spreading introduced species, such as *Megachile sculpturalis* (Mangum & Sumner, 2003; Roulston & Malfi, 2012).

Our data indicate that different bee species thrive best in different urban green space types. This suggests that complementary and collaborative planning of such space could be specifically designed to foster native species. More research is required on the impacts of different management plans and conservation actions to ensure that 'scaled up' urban habitat alteration has positive outcomes (Colding, 2007; Goddard et al. 2010). We have found that occupancy modelling provides additional details that are not discovered with detection and abundance-based sampling and conclude that they should be used as part of all biodiversity monitoring schemes.

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4.7 Tables

Table 5. A list of the six bee species studied and the model equation used to fit the presence-absence data for each, as collected over the three-year study period. The nesting tube widths used (the preferred width in bold), the observed frequency from the sample across all sites is also included.

Species	**Nest width**	**Actual Occupancy**	**Model Equation**
Introduced			
Megachile rotundata (Fabricius)	3.4, **5.5**, 7.6	0.337	Ψ(site),*p*(foot,site)
Megachile centuncularis (Linnaeus)	5.5, **7.6**	0.176	Ψ(foot),*p*(.)
Osmia caerulescens Linnaeus	3.4, **5.5**	0.342	Ψ(site),*p*(foot,site)
Native			
Megachile campanulae (Robertson)	**5.5**, 7.6	0.286	Ψ(site),*p*(.)
Megachile pugnata Say	5.5, **7.6**	0.045	Ψ(foot,site),*p*(site)
Osmia pumila Cresson	**3.4**, 5.5	0.322	Ψ(site),*p*(.)

4.8 Figures

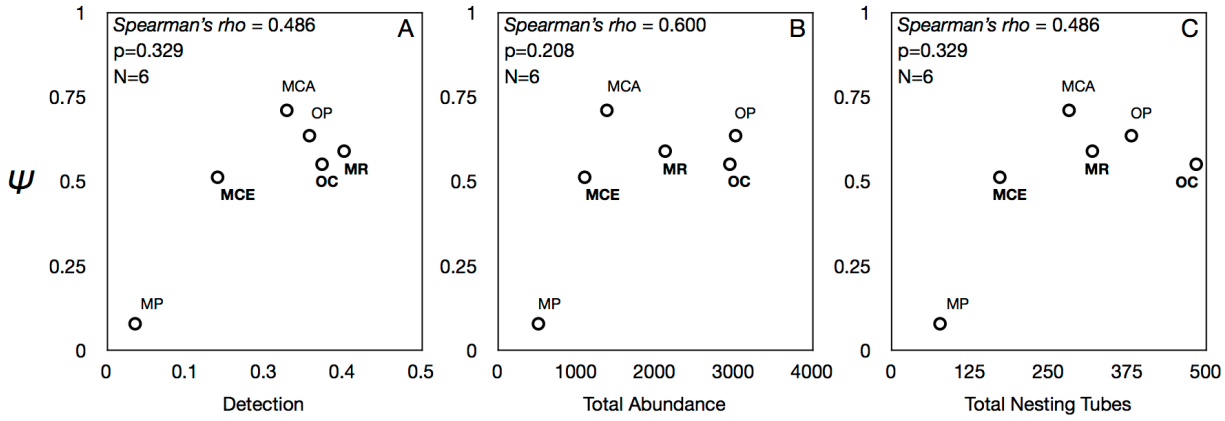

Figure 14. Rank correlations of all six species comparing occupancy probability estimates and (A) detection, (B) total abundance, and (C) number of nesting tubes for each species over the sampling period. Native species were *M. campanulae* (MCA) *M. pugnata* (MP), and *O. pumila* (OP). Introduced species were (in bold) *M. centuncularis* (MCE), *M. rotundata* (MR), and *O. caerulescens* (OC).

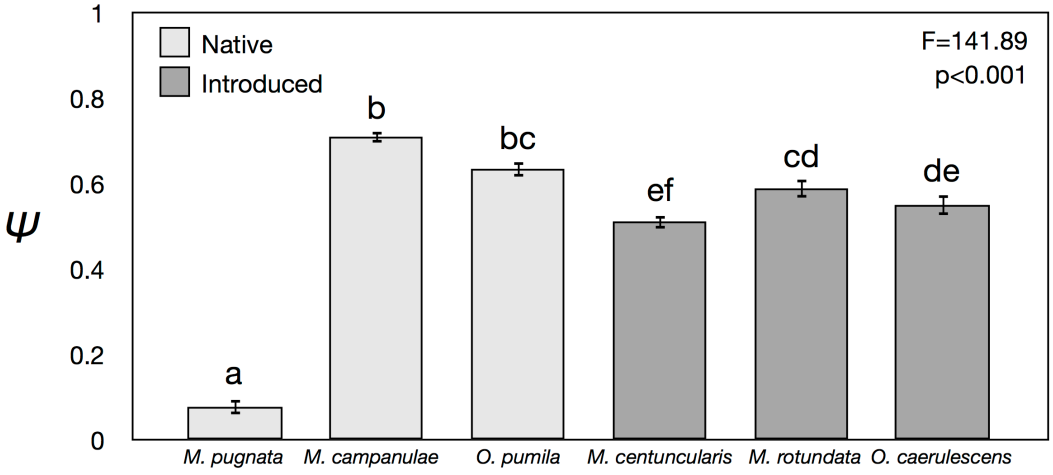

Figure 15. Occupancy probability compared between all six species. Significant differences (α=0.05) indicated alphabetically.

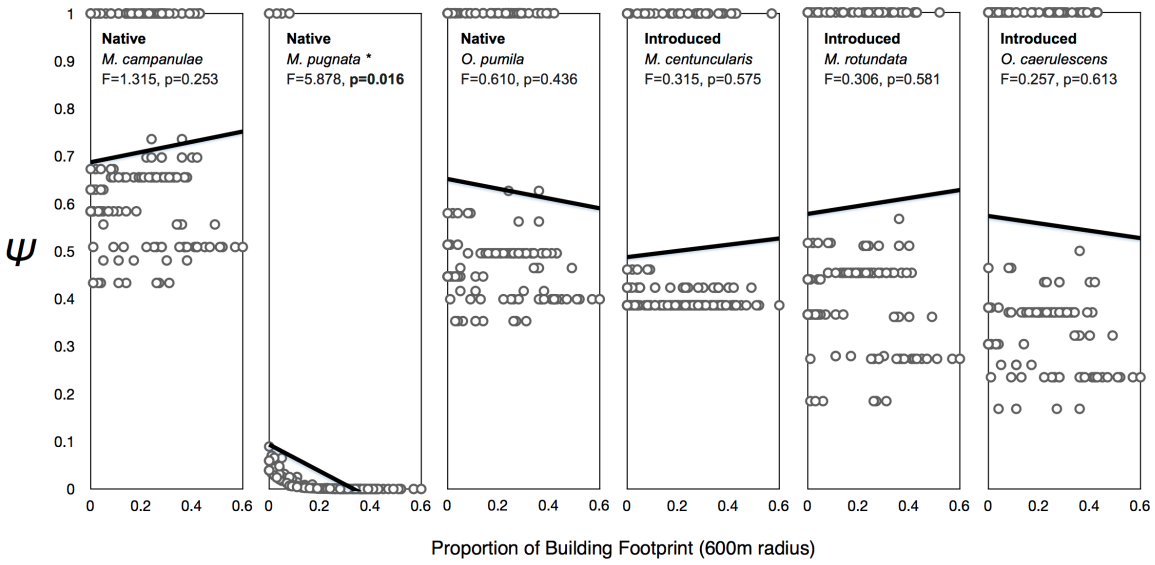

Figure 16. Occupancy probability per bee plotted against the proportion of building footprint within a 600m radius around each site. Significant differences calculated using the Z-score of building footprint. Asterisk indicates significant difference within species.

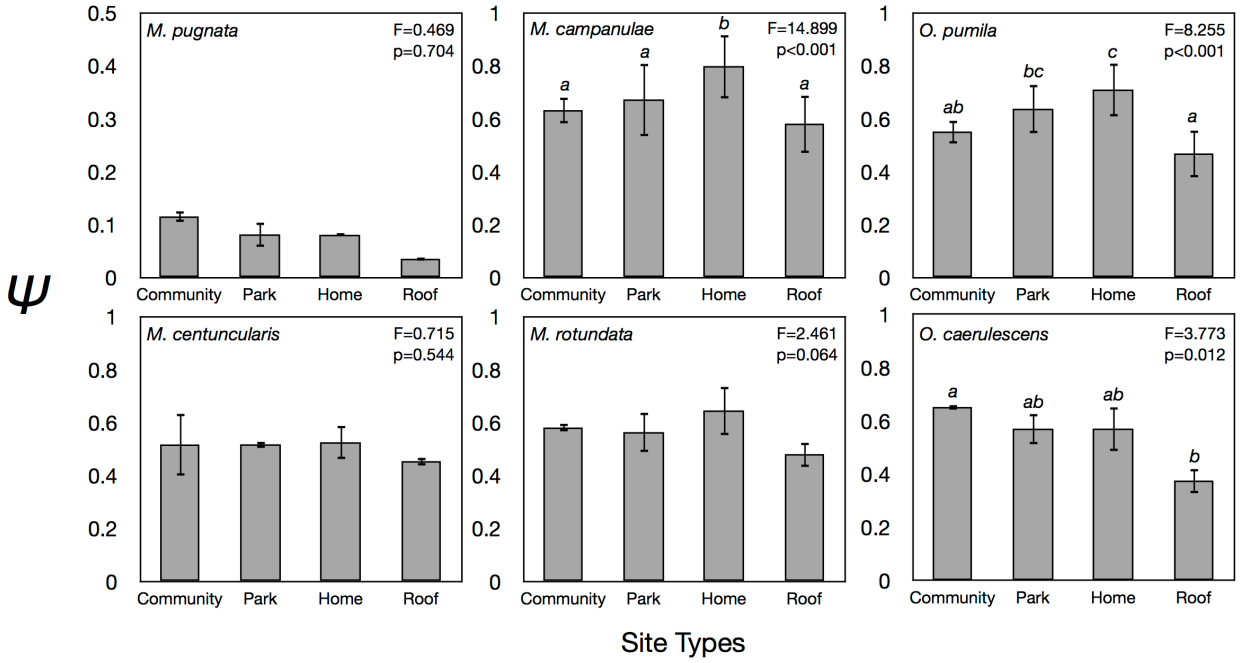

Figure 17. Mean occupancy probabilities of native (*M. campanulae, M. pugnata*, *O. pumila*) and introduced (*M. centuncularis*, *M. rotundata*, *O. caerulescens*) bee species when grouped by site: community gardens (N=14), building rooftops (N=20), city parks (N=43), and residential gardens (N=72).

Chapter 5: Bee hotels as tools for native bee conservation: A premature verdict?

5.1 Abstract

Society is increasingly concerned with declining wild bee populations. Although most bees nest in the ground, considerable effort has centered on installing 'bee hotels' – also known as nest boxes or trap nests – which artificially aggregate nest sites of above ground nesting bees. Campaigns to 'save the bees' often promote these devices despite the absence of data indicating they have a positive effect. From a survey of almost 600 bee hotels set up over a period of three years in Toronto, Canada, introduced bees nested at 32.9% of sites and represented 24.6% of more than 27,000 total bees and wasps recorded (47.1% of all bees recorded). Native bees were parasitized more than introduced bees and females of introduced bee species provisioned nests with significantly more female larva each year. Native wasps were significantly more abundant than both native and introduced bees and occupied almost ¾ of all bee hotels each year; further, introduced wasps were the only group to significantly increase in relative abundance year over year. More research is needed to elucidate the potential pitfalls and benefits of using bee hotels in the conservation and population dynamics of wild native bees.

5.2 Introduction

Bees and the pollination services they provide are in decline as a result of various anthropogenic activities that undermine bee foraging and nesting (Biesmeijer et al. 2006; Potts et al. 2010; Burkle et al. 2013; Ollerton et al. 2014). Concern for bees among the general public has led to increases in the numbers of novice beekeepers in urban centers (Moore et al. 2013) and augmentation of habitat for bees including the addition of both food (bee-friendly plants) (Pawelek et al. 2009; Matteson & Langellotto, 2011) and nest sites (bee hotels) (Gaston et al. 2005). The marketing of bee hotels to promote pollination and wild pollinator conservation is widespread and expanding, at least in North America and Europe (Jones, 2010). These structures, also known as trap-nests or nest boxes (Krombein, 1967), use some bee's preferences for nesting in above-ground cavities as arise naturally in a variety of settings such as pithy stems and beetle burrows in wood (Lee-Mäder et al. 2010; Vickruck et al. 2012). Bee hotels are usually made from bundled plant stems, paper-based tubes, or holes drilled in wood or molded in plastic; in all cases they artificially aggregate nesting sites above densities naturally available for cavity-nesting bees (Krombein, 1967) (Figure 18A-C).

Bee hotel development began in the 1950s when paper straws and wooden blocks with holes drilled into them were experimentally set out to house the alfalfa leaf cutter bee [*Megachile rotundata* (Fabricius)] in transportable and stackable containers (Krombein, 1967). At that time, farmers from Utah to Saskatchewan were encouraging this exotic species to nest in holes they had drilled into the sides of their own buildings (Bohart, 1972). Over the ensuing decades there has been an increasing diversity of designs available for purchase as ready-mades or through DIY instructions (e.g. http://www.xerces.org/). In agricultural settings, a variety of mason bees, in addition to the alfalfa leafcutter bee, have been managed successfully using bee hotels (Bohart, 1972; Bosch & Kemp, 2002; Pitts-Singer et al. 2011). These easily manipulated structures have also been used for ecological research (Steffan-Dewenter et al. 2002; Tylianakis et al. 2006;

Zurbuchen et al. 2010; MacIvor et al. 2014). Promotion of bee hotels in urban gardening as a means of supporting native pollinators is a more recent phenomenon. Here we investigate whether they do indeed support native pollinators rather than introduced ones or other organisms entirely. Specifically, we test the following hypotheses.

1. Compared to native bee species, introduced ones are more common in bee hotels. Introduced species often exhibit greater flexibility in habitat requirements (Lowry et al. 2013; Barthell et al. 1998), allowing them to colonize new environments; bee hotels may constitute such a novel environment.
2. Wasps (such as many solitary Vespidae) that seek out the same nesting cavities will be more common than native bees in bee hotels because wasps use widely available nesting materials to partition their nests (e.g. mud and grass) whereas bees use more site specific materials (e.g. tree resins and leaves of certain plants) (Krombein, 1967; Taki et al. 2004; Lee-Mäder et al. 2010).
3. Introduced species will be more common in bee hotels located in areas that are most heavily anthropogenically-modified. This is expected because recent studies that investigate urban insect diversity find introduced species to be the dominant taxa (Bolger et al. 2000; Matteson et al. 2008).
4. Compared to native species, introduced ones will have decreased rates of parasitism. This is a test of whether the enemy release hypothesis (Liu & Stiling, 2006) applies to bees that nest in bee hotels. In bee hotels, parasitism is greater compared with natural nesting sites (Wcislo, 1996) in part because aggregated nests create an easier search target for parasites (Rosenheim, 1990). This may exacerbate the differences in parasitism rates between native and exotic species.

If hypotheses 1, 3 and 4 were to be supported we could suggest the following two

additional hypotheses:

5. Introduced bees will show a greater increase in bee hotel use over time from year to year.

6. Introduced bees will exhibit greater population increase (expressed as number of females per nest tube) than native species.

We test these hypotheses with 200 bee hotels set up annually for each of three years within the city of Toronto, Canada. We test the first five hypotheses using all bees and wasps detected; the fifth and sixth were explored using two congeneric pairs of the commonest species found, in each case one member of the pair was introduced, the other native.

5.3 Methods

From May to October 2011-2013, 200 bee hotels were set up each year throughout the Toronto area (each bee hotel representing one 'site') to survey above ground nesting bees as described in Chapter 1 (Figure 18). The majority of sites were sampled all three years (73.7%), 16.9% were sampled over two years, and 9.4% were sampled in just one year. A bee that uses the hotel enters a suitable cardboard tube (the one that best fits her body dimensions) and constructs brood cells in a series from the back of the tube to the front (Stephen & Torchio, 1961; Krombein, 1967; Lee-Mäder et al. 2010). Bee hotels were set up individually at sites at least 250m apart, in four different urban green space types: community gardens, residential gardens, city parks, and building rooftops. Permission was granted to set up at each site after meeting with individual site managers or homeowners to discuss the research.

At the end of each field season, the bee hotels were collected, each cardboard tube opened and each brood cell removed, individually labeled and placed in storage to overwinter at

4°C. In April of the following year brood cells were moved to a sealed incubation chamber kept at 26°C and 65% humidity until adult emergence. They were then sexed and identified to species, permitting categorization of each individual as native or introduced to the study region (Cane, 2006; Giles & Ascher, 2006; Packer et al. 2015). All bees and wasps are stored at the Packer Collection at York University (PCYU). Over all sites and years, colonization (determined as presence in a bee hotel) and relative abundance (the proportion of all brood cells that were of the focal species per bee hotel) were compared between native and introduced bees (NB vs IB), native and introduced wasps (NW vs. IW), as well as among all four groups using linear regression analysis (GLM) (α=0.05) with a Tukey post hoc analysis in SPSS v21 (all analyses described hereafter used this program). Colonization and relative abundance of native bees (NB) were also compared with all potential competitors of native bees for nesting opportunities in bee hotels (introduced bees and introduced and native wasps grouped together; hereafter referred to as “AO”, as in “all others”) using a paired t-test. The same GLM test was used to determine whether colonization or relative abundance between native and introduced bees and wasps differed by site type.

The total number of parasites attacking bee and wasp brood were recorded by site, and the parasites reared and identified as accurately as possible using standard morphological approaches combined with DNA barcoding (Ratnasingham & Hebert, 2007). The total parasitism rate combining all brood cells over all three years were compared separately as before between native and introduced bees and wasps using GLM analysis with Tukey post hoc testing to distinguish between different bee and wasp groups. Although the bees and wasps we sampled were not released back to the site from where they were collected, to examine patterns in use over time, the abundance of each group per site were independently examined over the three years using a repeated measures ANOVA with data from the first year of sampling acting as a baseline for comparison. This was completed only for the sites sampled in all three years

(N=147).

We compared the sex ratio, as well as an estimate of the rate of increase in population size of the four most common bee species over the three-year study period. The most common bees were two native [*Osmia pumila* Cresson, *Megachile campanulae* (Robertson)] and two introduced species [*O. caerulescens* (L.) and *M. rotundata*] (Table 6). The estimate of population increase for each species was determined by comparing the number of female offspring provisioned by nesting females in 30 individual nests of the same nesting tube width dimension (1 per site; 10 sites selected randomly among those colonized by the species in all three years). The sex ratio (recorded as the proportion of females per nest) and the estimate of population increase over the study period were independently compared for two pairs of bee species using GLM testing and post hoc analysis.

5.4 Results

Of 600 bee hotel/years set up, data were obtained from 574 (186 were recovered in 2011, 194 in 2012 and 194 in 2013). We found a total 27,275 individuals including 31 species of pollinating bees [comprising 52% of all cavity-nesting bee species known from the area (Packer et al. 2015)] and an additional five cleptoparasitic bee species (36 bee species total) (Table 6). Ten of the species we found were not native to the region, representing 76.9% of the known introduced cavity-nesting bee fauna in southern Ontario (Table 6). The offspring generations of two introduced species: *O. caerulescens* and *M. rotundata* were particularly common; representing 20.7% and 15.4% respectively of the total number of bees reared over the entire study period.

There was no significant difference between native and introduced bees in the number of sites occupied (Figure 19A), with introduced bees nesting in bee hotels at an average of 32.9% of sites per year (native bees: 39.8%). Native bees colonized significantly fewer sites than did all other groups combined (AO: 70.5%) (Figure 19B).

There was no significant difference in the relative abundance of introduced and native bees reared from bee hotels (Figure 19C); introduced bees represented 47.1% of the total number of bees reared (56.9% for native bees), and 24.6% of all bees and wasps reared (27.6% for native bees). However, the relative abundance of native bees was significantly less ($t=9.239$, $p<0.001$) than that of all competing groups combined (AO: 72.4%)(Figure 19D). Native wasps were significantly more abundant than any other group (Figure 18A; $F_3=20.46$, $p<0.001$) and comprised 37.8% of all bees and wasps reared from bee hotels.

The type of urban green space was a significant determinant of the abundance of native bees ($F_3=5.369$, $p=0.001$, greatest in residential gardens), introduced bees ($F_3=4.511$, $p=0.004$, greatest on rooftops, and to a lesser extent community gardens) and native wasps ($F_3=5.880$, $p=0.006$, greatest in urban parks), but not of introduced wasps (Figure 20). Significantly more native bees were parasitized compared to introduced bees ($t=13.904$, $p<0.001$) (Figure 21), although parasitism rates did not differ between introduced and native wasps.

Repeated measures analysis showed that there was no significant change in relative abundance of native or introduced bees or native wasps year-over-year; however, there was a significant increase in introduced wasps ($F_3=6.555$, $p<0.001$) (Figure 19C).

Finally, the sex ratio as determined by the number of females provisioned per preferred nesting tube width in the two pairs of native and introduced bees species was significantly more skewed towards females in introduced than native bees ($F_3=28.683$, $p=0.033$) (Figure 22A). This trend was driven by one native, *O. pumila*, which provisioned, on average, half as many females as the other native (*M. campanulae*) per brood cell. *Osmia pumila* was the only bee among the four to prefer the 3.4mm nesting tube width (73.1% of all nest tubes occupied and 77.1% of all brood produced). The average number of female offspring provisioned per female did not change significantly for any of the four species over the three years of study ($F_3=0.738$, $p=0.481$). However the estimate of the rate of population increase differed significantly among

species with both introduced bees (*M. rotundata, O. caerulescens*) and one native (*M. campanulae*) provisioning significantly more female offspring per nesting female compared to native *O. pumila* (F_3=25.636, p<0.001) (Figure 22B).

5.5 Discussion

We investigated the relative use of bee hotels by native and introduced bees and wasps to assess the potential of these novel habitat augmentation schemes for increasing populations of native bees. Several lines of evidence suggested that native bees performed comparatively poorly.

First, although there was no difference in the abundance or colonization of bee hotels by introduced and native bees, native bees were in the minority, representing 27.7% of all bees and wasps reared (AO + NB). Thus, our hypothesis that introduced bees would use the hotels more often than native bees was rejected. This result was similar to that found in a study in California where native bees or wasps never amounted to more than 25% of bee hotel occupants over two years (Barthell et al. 1998). Grouping all potential competitors of native bees for nesting opportunities in bee hotels (AO), we found that their colonization rate and abundance was greater than that of native bees. Native wasps were significantly more abundant than native and introduced bees, and so our second hypothesis, that wasps could outcompete bees for these nesting structures was supported. Our third hypothesis - that site type, as determined by the type of urban green space where the bee hotel was installed - would influence the relative abundance of native bees was supported. Bee hotels in residential gardens had significantly more native bees (e.g. Lowenstein et al. 2014) while more anthropogenically-modified sites (e.g. vegetated rooftops) supported significantly higher numbers of introduced bees (Figure 20).

Our fourth hypothesis was that introduced bees would be parasitized less often than native bees. This pattern was evident when all years were combined (Figure 21) and so we

accepted our fourth hypothesis. From the repeated measures analysis and using the first year of abundance data per sites as a baseline for comparison, no significant difference in changes in abundance was evident from year to year for native or introduced bees, and we rejected our fifth hypothesis.

Our sixth hypothesis that introduced bees would exhibit greater population increase than native bees was partially supported. Our most common native bee, *O. pumila*, provisioned significantly fewer females per nest than did either of our two introduced bees (Figure 22). *Osmia pumila* preferred smaller diameter nesting tubes than did our other three species and because males are smaller than females use of smaller diameter tubes is expected to result in a more male-biased sex ratio. For example, an increasingly male biased sex ratio was reported for *Osmia lignaria* in smaller sized nesting tube diameters (Torchio & Tepedeino, 1980). To check whether reduced female production by *O. pumila* might have been an artefact of tunnel width preferences we looked at its sex ratio in tubes of both diameters. In 3.4mm tubes, 7.9% of the brood was female whereas in 5.5mm tubes 58.6% were females giving a total of 19.5% female overall in the population of *O. pumila*. The other three species preferred to nest in the 5.5mm nesting tubes (*M. campanulae* = 81.3% of all brood reared, *M. rotundata* = 60.2%, *O. caerulescens* = 77.8%).

Altogether, our study findings show that bee hotels appear to differentially augment populations of wasps rather than those of native bees, and introduced bees outperform at least some native bee species in some population parameters in bee hotels and in some urban green space types. These results highlight a need for increased study of bee hotels and their associated impact upon bee biodiversity and pollination in the urban setting.

One reason bee hotels are promoted is their potential for augmenting pollination of native plants (Kearns et al. 1998) and/or crops (Garibaldi et al. 2011). However, introduced pollinators, which in this study represented almost half of all bees reared, are often the dominant or sole

pollinator(s) of introduced plants (Woodward, 1996; Morales & Aizen, 2002; Hanley & Goulson, 2003), whereas, native bees prefer native plants to alien ones (Williams et al. 2011).

At their worst, bee hotels may act as population sinks for bees through facilitating the increase of parasites, predators (e.g. Figure 18D-F), and diseases as a result of functional responses to unnaturally high nest densities and nesting site entrances set up in two-dimensions rather than in the more three dimensional arrangement found in nature (e.g. erect plant stems, decaying logs) (Wcislo, 1996). Bee hotels may be designed to encourage different bee species by varying nesting tube/hole width or length, but encouraging different bee species to co-aggregate in a bee hotel might inadvertently increase opportunity for parasites to attack related species: developing novel hosts or affect more susceptible species (MacIvor & Salehi, 2014). Although there has been little discussion of parasite loads obtained with different bee hotel designs (Lee-Mäder et al. 2010) in all cases where nesting sites and nesting bees are aggregated, the chance of parasites finding and attacking nests is increased (Rosenheim, 1990). Some bee hotels have thin-walled nest tubes that facilitate parasite transfer within the hotel, even by parasitic insects with short ovipositors such as generalist *Monodontomerus* wasps (Eves, 1970). This can result in mortality of entire hotel contents (Lee-Mäder et al. 2010). The relative influence of host aggregation was not examined in this study, however we did find a significant increase in the total number of parasites attacking native bees compared to exotic ones. These findings might have resulted from enemy release among introduced bees, which were free of specialist parasites that attack them in their native ranges (Liu & Stiling, 2006).

Given bee hotels could have a negative or a positive impact on their target organisms, an obvious question is: How can designs be modified to promote the desired outcomes? Finding answers to this would involve increased research on the parameters that vary among different bee hotel designs and their relative success at promoting native bees. This could include studies that manipulate the number, positioning/location, and materials used in bee hotel construction.

The impact of maintenance might include replacement of completed nesting tubes with new unoccupied ones to reduce within-season competition for nest sites. Matching the length or especially the width (Bohart, 1972; Lee-Mäder et al. 2010) of nesting tubes in bee hotels to that of preferred plant stems and beetle-bored holes in wood could reveal parameters that increase attractiveness to specific native bees, reduce rates of parasitism, and/or increase the number of females provisioned per nest [e.g. Stephen & Osgood, 1965; Torchio & Tepedino, 1980). For example, a nest tube diameter between 3.4mm and 5.5mm would seem to be necessary for population increase in *O. pumila.*

5.5.1. “Bee-washing”: A Call for Research

We advocate for due diligence on the part of retailers and promoters of bee hotels to avoid “bee-washing”; that is, green-washing (Walker & Wan, 2012) as applied to potentially misleading claims for augmentation of native and wild bee populations. To ensure “bee-washing” is minimized, it is imperative that more research be performed on the design and effectiveness of bee hotels. Bee hotels are useful for ecological and behavioral studies, outreach in citizen science and pollinator education campaigns. Sampling with them can even reflect the diversity of the larger bee community [e.g. including bees that nest in the ground (Westphal et al. 2008)]. However the magnitude of potential pitfalls noted above needs to be assessed through continued study, especially of the impact of hotels on native bee population dynamics. Such work would also provide detailed data on the pollen and nesting resources used, parasite associations, sex ratios, and behaviors.

Comparing nesting success in bee hotels with that at naturally occurring nesting sites (Potts et al. 2005; Torné-Noguera et al. 2014) could improve the effectiveness of this management tool and permit its integration into landscape planning practices targeting conservation. Specifically, through better designs modeled after natural conditions both in

materials used and details of positioning in the environment. At present, some bee hotels marketed for consumer use may act as sinks for their target organisms through provision of entirely inappropriate edaphic conditions as a result of the materials used. For example, some designs are simply holes drilled (or molded) into solid plastic blocks. It seems highly improbable that these designs will provide the same moisture balance as occurs in nature and increased moisture retention likely leads to increased brood mortality due to mold, which can represent a large proportion of total brood mortality (Packer & Knerer, 1986). Set up and orientation could also be linked to attractiveness to native bees, especially versus wasps (e.g. Martins et al. 2012); for example, solitary wasps can be more prevalent in bee hotels placed in shaded conditions (Taki et al. 2004). These wasps may provide important services to urban gardeners as predators of pests (Grissell, 2010), but compete with bees for nesting space in bee hotels. This suggests the need for a deeper understanding of the relative importance of the pollination augmentation versus pest control potential of bee hotels. In sum, we advocate for more research and increased responsibility on the part of retailers and advocates of bee hotels so that these structures are designed and managed to minimize negative effects and become truly useful tools for conservation biologists and conservation-minded citizens.

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5.7 Tables

Table 6. List of all bee species recorded in the study area per year (Y: yes; N: no). Bolded species are introduced to the study region. Missing introduced cavity-nesting bees known from the region included: *Anthidium oblongatum* (Illiger), *Hoplitis anthocopoides* (Schenck), and *Megachile ericetorum* Mitchell.

Family	Genus	Species	2011	2012	2013
Apidae	*Anthophora*	*terminalis* Cresson	N	N	Y
Megachildae	*Megachile*	*brevis* Say	N	Y	N
		campanulae (Robertson)	Y	Y	Y
		centuncularis (Linnaeus)*	Y	Y	Y
		frigida Smith	N	Y	Y
		inermis Provancher	Y	N	N
		mendica Cresson	Y	Y	N
		pugnata Say	Y	Y	Y
		relativa Cresson	Y	Y	Y
		rotundata Fabricius	Y	Y	Y
		sculpturalis Smith	N	N	Y
	Heriades	*carinata* Cresson	Y	Y	Y
		variolosa (Cresson)	Y	N	N
	Chelostoma	*campanularum* (Kirby)	N	Y	Y
		rapunculi (Lepeletier)	Y	N	Y
	Hoplitis	*producta* (Cresson)	Y	Y	Y
		spoliata (Provancher)	Y	Y	N
		truncata (Cresson)	N	N	Y
	Osmia	*pumila* Cresson	Y	Y	Y
		caerulescens (Linnaeus)	Y	Y	Y
		lignaria Say	Y	Y	Y
		atriventris Cresson	N	Y	N
	Anthidium	*manicatum* (Linnaeus)	Y	N	Y
	Coelioxys	*alternata* Say +	Y	N	N
		moesta Cresson +	N	Y	N
		sayi Robertson +	Y	Y	Y
	Stelis	*lateralis* Cresson +	Y	Y	N
		vernalis Mitchell +	N	Y	N
Colletidae	*Hylaeus*	*affinis* Smith	Y	Y	Y
		annulatus (Linnaeus)	Y	Y	Y
		hyalinatus Smith	N	Y	Y
		leptocephalus Morawitz	N	Y	Y
		mesillae (Cockerell)	Y	N	Y
		modestus Say	Y	Y	Y
		punctatus Brullé	Y	Y	N
		verticalis (Cresson)	N	Y	N

* *M. centuncularis* status is not clear, with Giles and Ascher (2006) denoting the species as introduced. + denotes species that are cleptoparasites.

5.8. Figures

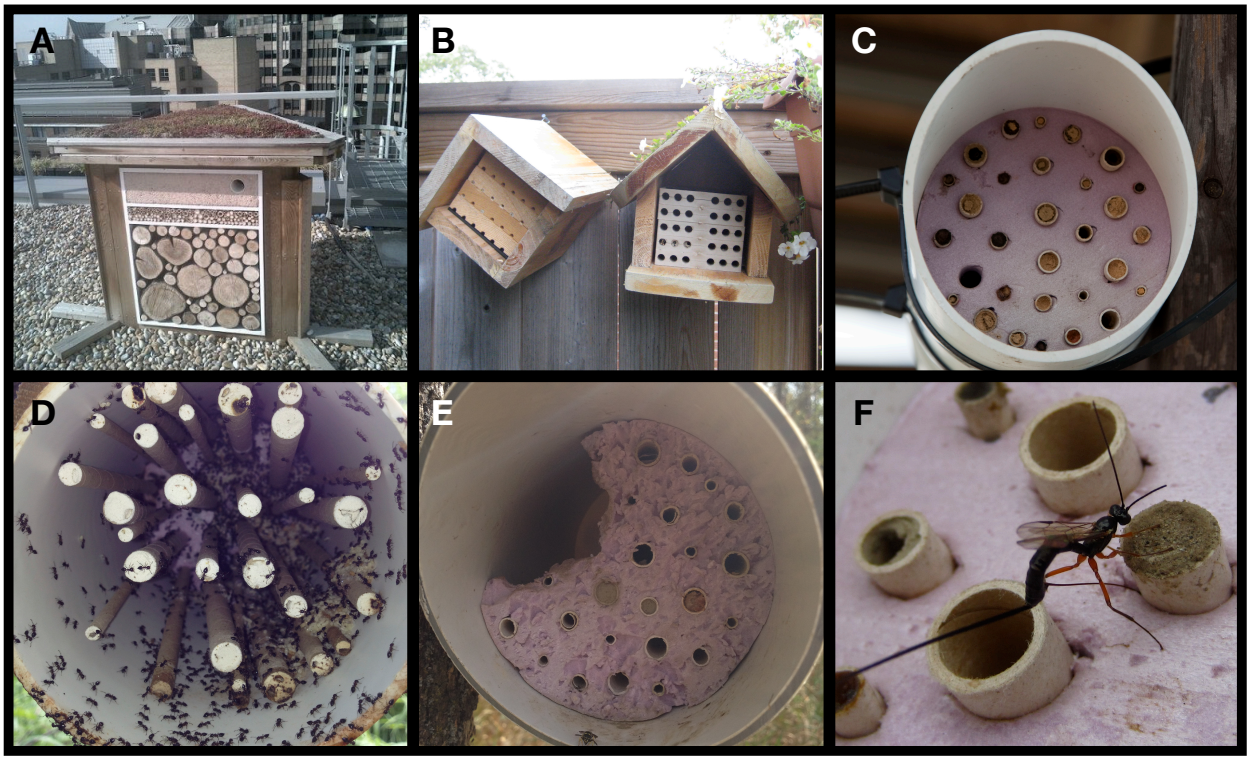

Figure 18. A. Bee hotel on a rooftop in London, UK (Photo: Thierry Spiess). B. Cartridge-style hotels made by bundling wood (left) or plastic (right) cartridges having drill holes along one edge for opening, inspecting and cleaning. C. Bee hotel having different nesting tube widths made of cardboard and enclosed in a PVC pipe for protection (Photo: Ed Snodgrass). D. Ant colony (*Tetramorium caespitum*) that took over an unmaintained bee hotel. E. An ichneumonid wasp parasitizing Osmia sp. through a cardboard nesting tube. F. Damage to the faceplate and nesting tubes in a bee hotel by an unknown bird.

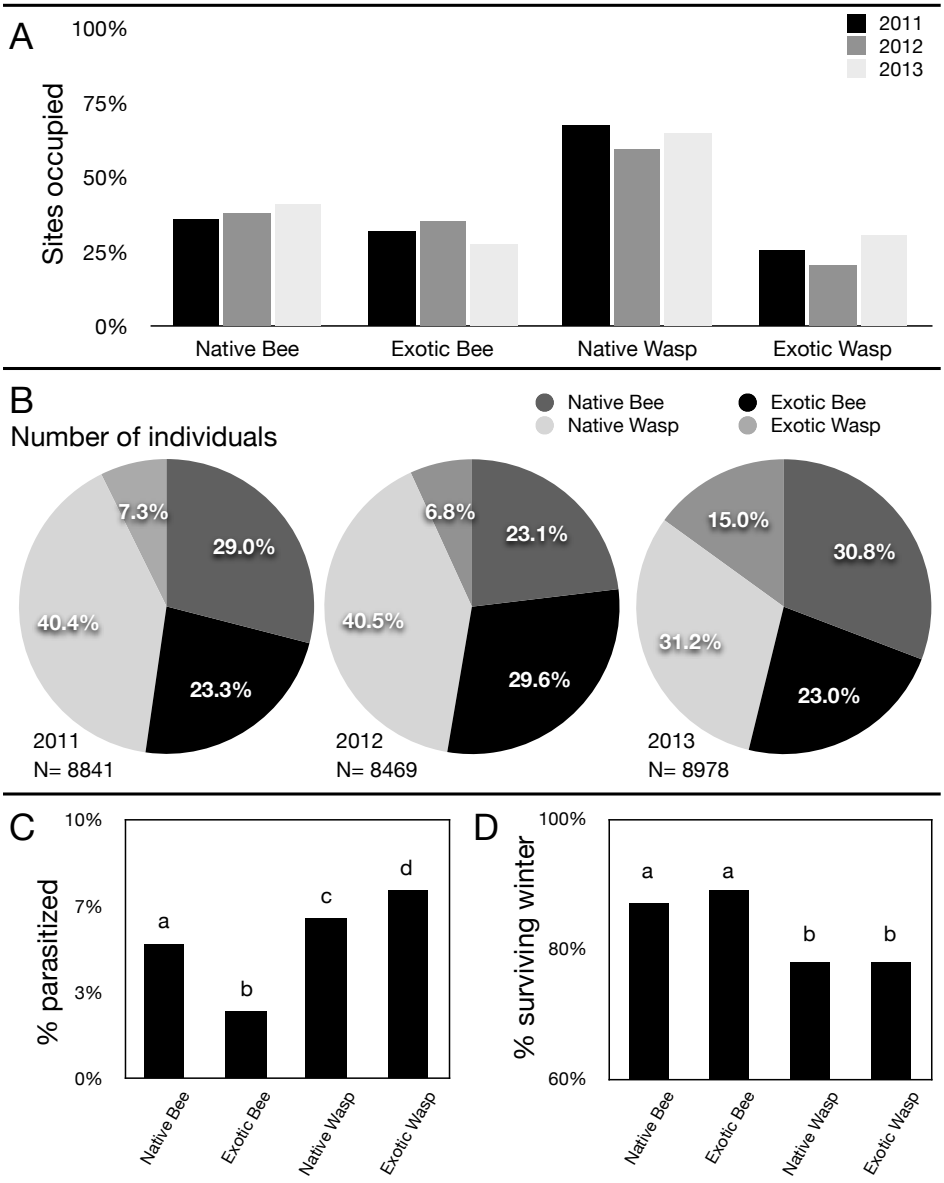

Figure 19. Presence and abundance of bees and wasps over all sampling years. A. The number of sites occupied by native bees (NB), introduced bees (IB), native wasps (NW) and introduced wasps (IW) over three years at over 600 bee hotels set up through out the city of Toronto and the surrounding region. B. Comparison of the number of sites occupied by NB and the other groups competing for nesting space combined (AO). C. The total number of brood cells produced in bee hotels per year by native and introduced bees and wasps, and D. shows a comparison between native bees and the remaining groups combined. Lower-case lettering indicates significant differences and in all graphs hereafter.

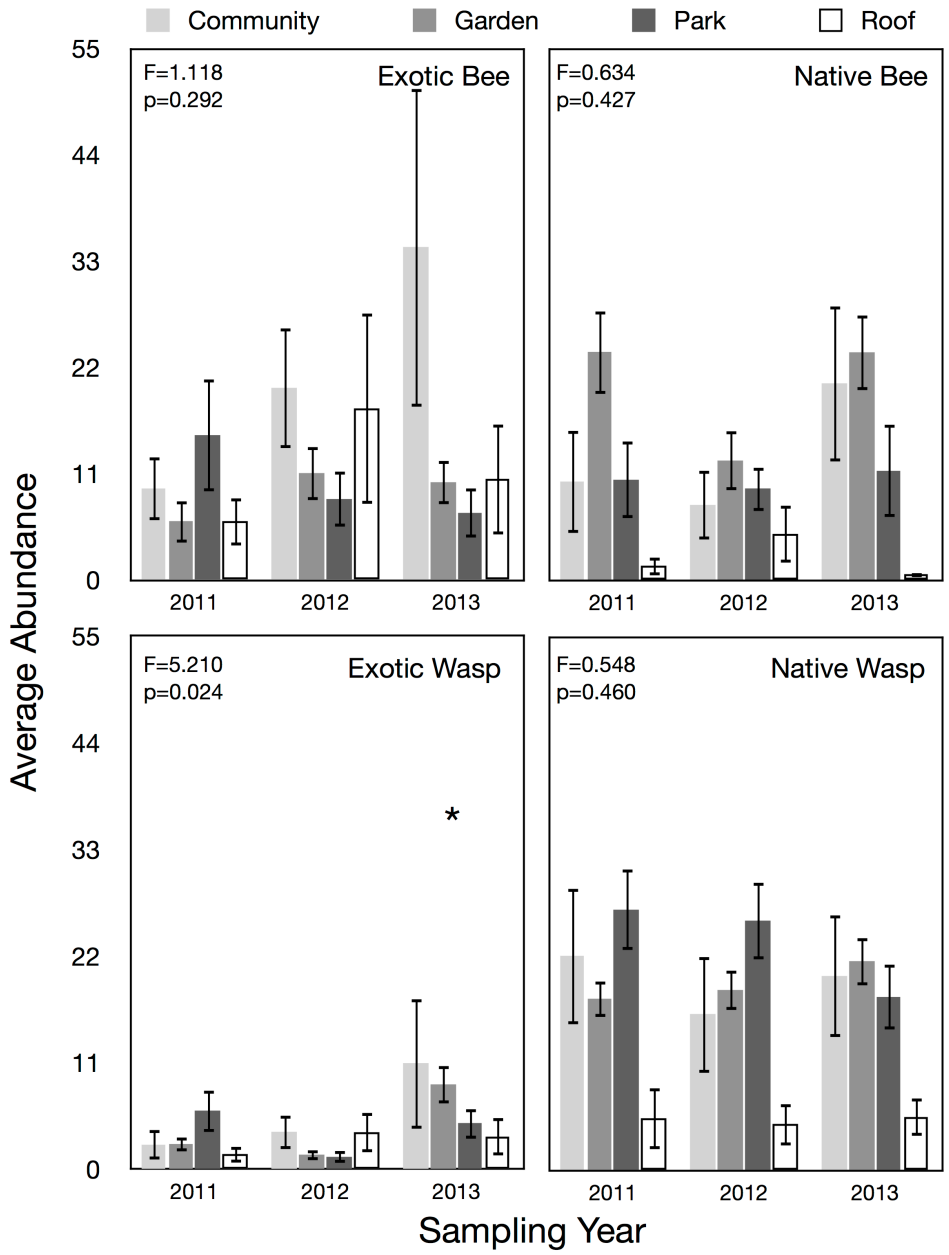

Figure 20. Mean relative abundance of bees and wasps at all site types over all years. Lower-case lettering indicates significant differences.

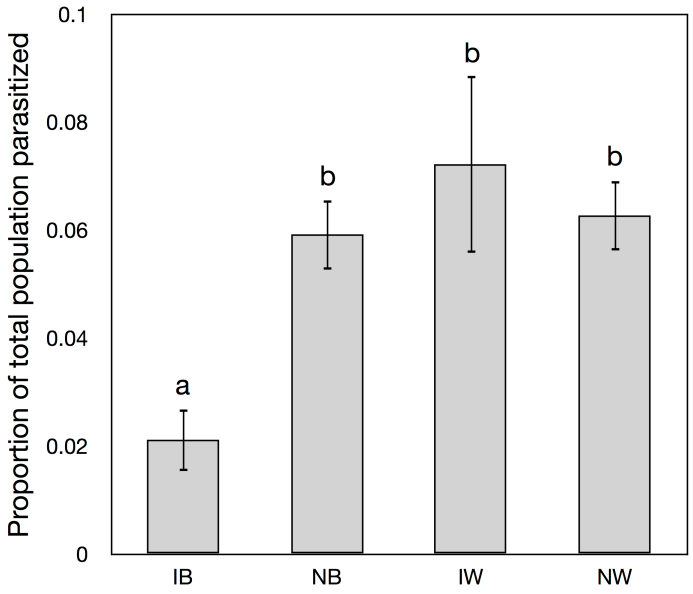

Figure 21. The proportion of parasitized brood cells from all sites and years combined.

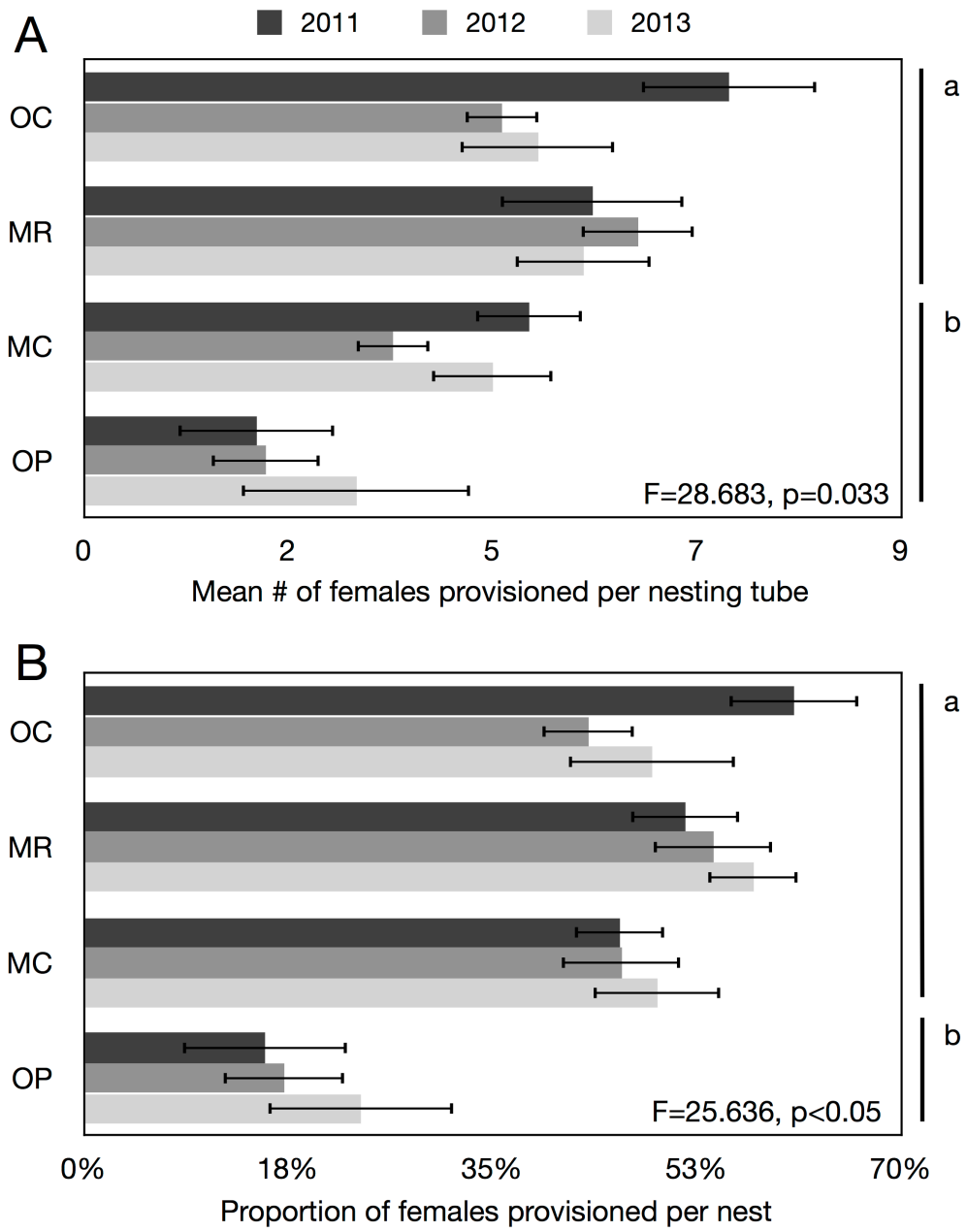

Figure 22. Number of females provisioned in nests by the most common native and introduced bees. A. Differences in the mean number of females in nests of four bee species [two introduced: *Osmia caerulescens* (OC), *Megachile rotundata* (MR); and two natives: *Osmia pumila* (OP), *Megachile campanulae* (MC)]. B. Estimates of the rate of population increase in those same bees as determined by the number of female offspring provisioned per individual nesting female over three years. Lower-case lettering reflects significant differences.

Chapter 6: Summary of main outcomes in research and outreach

6.1 Research findings

Nest boxes are useful tools for monitoring bees and wasps and provide a plethora of information regarding their ecology, diversity, and behaviour. Since nest boxes are low cost and require little within season maintenance, habitats of interest can be saturated with nest boxes and data collected across large areas. These data can be used to examine environmental change and impacts on biodiversity. In this dissertation it was shown that in cities, both ecological and socioeconomic factors impact bees and wasps. Monitoring these taxa can inform our urban wildlife planning, as well as research into broader questions in landscape and urban ecology. In a review of the literature using nest boxes I found that less than 5% of studies sample urban environments (Appendix B). Although urban environments are increasingly a focus in ecological research (Niemelä, 1999; Pickett et al. 2011; Grove et al. 2014; Hahns & Evans, 2015; Pataki et al. 2015), there remain considerable gaps in understanding patterns in diversity and abundance of urban bees and wasps.

In this dissertation, I recorded 84 species of bee, wasp, and parasite species from nest boxes set up in Toronto and the surrounding region (Chapter 2). This is to my knowledge the most species recorded from any published study on cavity-nesting bees and wasps using nest boxes. Half of all colonizers were wasps, and the most abundant species were exotic bees, *Megachile rotundata* and *Osmia caerulescens*. However, more native bee species were recorded in nest boxes than exotic species (Chapter 5), presumably because there are more native cavity-nesting bees than exotic ones present in the region (Packer et al. 2015).

At the community level, bee and wasp richness and abundance tended to decline with increasing urbanization; however, some species (e.g. *Megachile rotundata*) increased in presence and abundance with urbanization. The type of urban green space surveyed and the

proportion of available habitat were important factors in increasing nest box colonization. Nest box diversity and abundance and in particularly that of bees responded positively to the indirect influence of the 'luxury effect', while wasps and parasites responded negatively to increasing human population density (Chapter 2). Using occupancy modelling to estimate presence of the most common bees where sampling indicated they were absent illustrated how some species could be more widespread than what is interpreted from abundance-based data alone. Specifically, occupancy modelling showed that the fourth most common bee, the native *M. campanulae*, was the most widespread (Chapter 4). More study is needed to elucidate the traits that increase urban tolerance among wild bees and other insects.

Using nest boxes often requires the collection and study of the bee and wasp larvae from within nest tubes. Increasingly there are tools to identify them to species (e.g. DNA barcoding), but more often than not they need to emerge to adulthood to permit their identification. Measuring emergence timing also permits other research opportunities regarding larval development, behaviour, and parasite activity. In this dissertation I quantified emergence timing within the community to further improve rearing methods and understanding seasonality and competition within the cavity-nesting bee and wasp community (Chapter 3).

The data produced in this PhD dissertation work were immense and diverse, leading to several other related projects that I published in peer-reviewed journals. Four first-author publications written using these data are included as appendix items (Appendix M-P).

6.2 Outreach

This thesis dissertation demonstrates the value of engaging citizen scientists to increase data sampled from large urban landscapes. Population density is high in urban areas and so large numbers of active participants can be included in studies (Silvertown, 2009; Dearborn and Kark, 2010). Without engaging the participants in this study, it wouldn't have been possible to set up

and monitor all 200 nest boxes, which were >250m apart, given the difficulty in travelling between sites (e.g. Toronto traffic) and coordinating access at private sites (e.g. requiring a resident, garden or building manager present).

Unlike other citizen science based projects that depend on opportunistic sightings of the species or taxa of interest (Strien et al. 2013), using nest boxes as fixed sites for observation meant that rather than identifying species, participants could observe colonization rates by monitoring the nesting tubes as they filled up. Participation in the study meant committing to the project over three years. During this time, I was able to cultivate relationships and more meaningful discussion about bees and their ecological functions with individuals. Simultaneously, these nest boxes became catalysts for conversation between participants and neighbours regarding wild bees and their needs, scaling up education, concern, and care for wildlife (Goddard et al. 2010).

Lastly**,** although only one nest box design was used, the design of nest boxes and their attractiveness to colonizing bees and wasps became an important topic of research for me beyond the dissertation work. This was especially the case at the beginning, during the development of the final nest box design (Figure 2) with Dr. Cory Sheffield and Dr. Peter Hallett. Delving into the history and design considerations of nest boxes led me to give several talks and nest box building workshops with school children, community and master gardeners, and other related groups (Appendix K). The greatest opportunity came in Sepember 2014 when I was offered to develop and teach a research seminar on bee habitat design in the Masters of Landscape Architecture program at the University of Toronto. The student works resulted in an art installation, and features in leading Architecture magazines. It is a win-win for ecological researchers to engage and collaborate with local citizens and non-science communities (Felson, 2013). Multi-disciplinary feedback and discussion greatly improved my ability to communicate the research findings to new audiences. This led to global collaborations, as well as new and

novel research directions in which I intend to push the intersection of ecology, biodiversity, and urban planning forward.

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Appendices

Appendix A. A sample 'call for participants' information sheet used to obtain study participants.

Wild bees in Toronto's green spaces

Pollination is an essential ecosystem service required to sustain flowering plant diversity. Unfortunately, pollinator diversity is declining worldwide, especially that of bees. Whereas considerable attention is given to the decline of managed honeybees, few have assessed the decline of wild bees, their pollinating services, and whether it is possible to enhance their presence through habitat creation and management. There is evidence that wild, solitary bees, including cavity-nesting bees which nest in an assortment of small holes, can persist in urban habitat altered by human activity; however, the ecological diversity of wild bees, their movement between patches, and how to manage their populations and pollination services remains greatly misunderstood. The objectives of this study are to quantify the direct and indirect local and landscape effects limiting wild, cavity-nesting bee biodiversity movement between urban habitat fragments. The goals are to obtain a spatial understanding of wild bee biodiversity for the city of Toronto to connect urban land use and building design strategies, such as green roofs, more directly to bee populations, and inform conversation on international bee declines and monitoring protocols.

Nestboxes

The primary method of assessing Toronto's cavity-nesting bee diversity will be nestboxes setup throughout the city. Each nestbox (35.6cm x 10.2cm) contains 25 holes of various widths, each of which may house 1 – 16 larva (next year's brood) provisioned by a variety of hard-working solitary female bee species. Since these bees work entirely on their own, there is no concern of attracting heaps of bees to your property. Moreover, few solitary bees can sting and those that can, generally don't - unlike honeybees, wasps, and bumblebees, solitary bees do not have large nests, queens, or stores of honey to defend. The nestboxes are small, maintenance-free, and allow for non-destructive sampling of bee diversity. Each bee will be identified to species as it emerges in the lab, and released back to the site from which they were provisioned at two intervals the following year.

How YOU can participate

Let us set up a nestbox in your front- or backyard, green roof, allotment plot, or community groups' food garden. Participation includes written permission to set a nestbox at your site in April, which we will remove in October. We'll also need access to the site to (non-intrusively) record vegetation, landscape, and climate data once per month (or more if necessary). The degree to which you participate is entirely voluntary, but you and anyone else you know are more than welcome and encouraged to take photos, or notes on activity at the nestbox that might be included in the study

Benefits of participating

- Be a leader in pollinator stewardship for your neighbourhood and the city of Toronto.
- Receive a complete diversity and abundance evaluation of the flowering plants and wild bees at your site, summarized annually.
- A free nestbox, increasing pollination activity at flowering plants in your yard.
- Reports on the entire project available by request, at workshops and at lectures in Toronto.
- Opportunities to experience firsthand the pollinators that occupy Toronto's green spaces.

Appendix B: REVIEW ARTICLE: Artificial nests for solitary bees, wasps, and their services: A century of design and motivation

1. Abstract

Solitary cavity-nesting bees and wasps are widely sampled using nest boxes. These devices aggregate nest sites for species that nest in pre-existing holes where brood cells are constructed in linear series. In nature these include hollow plant stems or bored holes in wood. Nest boxes are analogs of natural nesting sites that are created by bundling stems, drilling holes into wood, or an assortment of other design types. Nest boxes were originally conceived to observe bees nesting and soon after to enhance populations for agricultural crop pollination. In the last century, they became important monitoring tools for research in many environments. From 360 publications, I examine the taxa investigated, habitats studied, nestbox design, motivations for and gaps in research using nest boxes. I discover that the majority of studies were concerned with bee rather than wasps or both taxa combined. As expected, agricultural areas were the most studied habitat type and many were motivated to enhance numbers of bees in the genus *Osmia* and *Megachile*. Most investigations were motivated by questions pertaining to the nesting biology of target taxa (41%) but also regional diversity of bees and wasps (18%), and the impact of local landscape factors on colonization (13%). Few studies used more than one nest box design type and design has varied considerably geographically and over the century. Drilled holes in wood (48.3% of studies) or dried and bundled reeds (39.5%) were most common. Nest boxes provide many opportunities for alternative pollinator and pest management in agriculture, landscape design, and to address more complex questions in applied and community ecology.

2. Introduction

Numerous survey methods and sampling tools are available to study bees and wasps in their natural habitats. Some of these techniques sample broadly taxonomically, such as pan traps (Kearns & Inouye, 1997), window traps (Rubene et al. 2015), malaise traps (Darling & Packer, 1988), sweep netting (Richards et al. 2011), or observations on flowers (Wilson & Thomson 1991). Other surveys target certain taxa by designing analogues of their nesting habitat. For example, Fussell & Corbet (1992) made wood and clay-brick nest sites for bumble bees (1.5% colonized of N=654 over 3 years), Sheffield et al. (2014) set out overturned flower pot saucers ("nesting saucers") for ground nesting *O. inermis* (Zetterstedt)(10% colonized of N=60) and Silva et al. (2014) used plastic bottles treated with propolis and wax to attract nesting colonies of stingless bees (5 species, 3.5% colonized of N=720 traps over two years).

Far greater success has been documented in attracting the intended taxa using nest boxes, which are built and set out to sample cavity-nesting bees and wasps (Krombein, 1967; Bosch & Kemp, 2002; Tylianakis et al. 2005; Westphal et al. 2008; Holzschuh et al. 2009; MacIvor et al. 2014). Bees and wasps using nest boxes are solitary and individually provision single brood cells in a linear series. As central place foragers, once a suitable nesting site is found, they will forage within a range around this site (Zurbuchen et al. 2010a), provisioning the nest with the various resources they seek (Peterson & Roitberg, 2006).

Cavity-nesting bees and wasps naturally nest in hollow plant stems, or holes in wood or other structures above ground (Figure A1). Nest boxes are made of these natural and regionally occurring materials or artificial ones providing analog cavity-like conditions and individual nesting tubes are often bundled together (Lee-Mäder et al. 2010). Nest boxes offer standardized nest site conditions that can be replicated for monitoring areas of interest (Tscharntke et al. 1998; Loyola & Martins, 2006). Populations can be manipulated by moving colonized nest boxes between sites or by altering nestbox orientation or positioning, the number of nesting tubes,

species, or parasites. In sum, flexibility in the use of nest boxes allows for elegant, low-cost sampling to address questions to do with impacts of environmental variables on visits to flowers by bees (Schüepp et al. 2011), prey collection by wasp (Ercit, 2014), diversity (Steffan-Dewenter et al. 2002; Westphal et al. 2008; Steckel et al. 2014), offspring production (Williams & Kremen, 2007; Steffan-Dewenter & Schiele, 2008) and many other topics.

Observational studies on natural nesting cavities of bees and wasps are dependent on search effort required to locate sufficient numbers of nests (e.g. Scott, 1993; Hurst et al. 1997; Sears et al. 2001) and could be improved by monitoring using nest boxes. For example, Matthews (2000) recovered 23 nests of *Psenulus interstitialis* Cameron to examine nesting biology from internodes of bamboo stems growing naturally on Magnetic Island, Queensland, Australia. Dobson & Peng (1997) collected nests of *Chelostoma florisomne* (Linnaeus) from dried stems of *Phragmites* comprising a thatched roof on an old farm in rural Sweden. Others document the nests of bees in the stems of different plants, such as *Ceratina mikmaqi* Rehan and Sheffield and *C. calcarata* Robertson in *Dipsacus fullonum* (Teasel), *Rubus strigosus* (American Raspberry), and *Rhus typhina* (Staghorn Sumac) (Vickruck & Richards, 2012) or *Augochlora esox* (Vachal) in the bromeliad, *Aechmea lindenii* (Zillikens et al. 2001). Observing bee and wasp species nesting in natural conditions can inform the selection and use of natural materials and the design of artificial ones.

Nest boxes are useful for ecological and behavioural research in most terrestrial environments, and especially agricultural landscapes. One requirement of a managed bee species for crop pollination is its acceptance of nesting habitat that can be set up and dismantled where required. Thus nest boxes can help identify potential species for management as alternative pollinators (Parker and Frohlich, 1983; Torchio et al. 1987; Wei et al. 2002; Wilkaniec et al. 2004; Sheffield et al. 2008b; West & McCutcheon, 2009). Nest boxes can also survey regional diversity (O'Neill & O'Neill, 2010), document introduced species (e.g. *Osmia tanneri*

Sandhouse: Torchio, 1984), and the spread of introduced species (e.g. *M. sculpturalis* Smith: Mangum and Sumner, 2003, *Isodontia mexicana* (Saussure): Scaramozzino et al. 1991; Ćetković et al. 2012).

Many factors impact the effectiveness of nest boxes as tools for sampling different bee and wasp taxa. These factors include the materials used in construction, nesting tube dimensionality, and the positioning, orientation, and timing of placement in the environment (Krombein, 1967; Budrienė et al. 2004; Lee-Mäder et al. 2010; Everaars et al. 2011). In general there is no consensus on best practices because many bee and wasp species have different preferences, but also because most researchers develop their own designs or borrow that of colleagues based on regionally available materials (Dicks et al. 2010). Increasingly, nest boxes are designed as products for sale to gardeners to enhance bee populations (MacIvor & Packer, 2015). This has greatly added to the diversity in material and design, as well as users and landscape conditions where setup (e.g. home gardens, urban agroecosystems, rooftops) (Westrich, 1996; Wilson et al. 1999; Gaston et al. 2005; Everaars et al. 2011; MacIvor, 2015). In this way, market demands, ecological research, and industrial design can collaborate on nest box formats that best target agricultural application and/or research, conservation, and public engagement objectives.

Here I review the peer-reviewed literature on the topic of nest boxes that studied cavity-nesting bees and wasps over the last century. I tabulate, analyze, and critique the design typology, habitats studied, motivations for using nest boxes. A goal in conducting this review is to highlight to readers the broad applicability of nest boxes as survey tools for bees and wasps, to enhance target species for pollination or pest control in agroecosystems, to study behaviour and ecology, and to engage local communities with wild (e.g. non-honey bee) pollinators.

3. Methods

Information on the use of nest boxes in studies of cavity nesting bees and wasps was compiled from the peer-reviewed literature using conventional journal article search engine tools including Web of Science, JSTOR, and Google Scholar (search terms: “bee” OR “wasp” AND “nest box/nestbox/trap nest/cavity nesting/hotel/condo”). Only experimental investigations were included. This search led to a total of 360 studies being discovered (Appendix C). For each I determined the geographic location of where the nest box sampling occurred, the habitat type investigated, whether the authors were interested in bees, wasps, or both, the number of types of nest boxes used and the material and dimensionality (diameter and length) of nesting tubes, and finally, the motivations for the research. A regression analysis was used to examine the change in the number of research publications using nest boxes over time. An analysis of variance was used to compare the number that focused specifically on bees, or wasps, or both. All statistical testing was completed using SPSS v 22.

4. Results and Discussion

The number of research publications on cavity-nesting bees, wasps, and both, all increased significantly over time from 1922 to today, the greatest increase coming from bee research (Figure A2). The majority of publications described sampling that was carried out over one (N=179) or two (N=71) seasons (Figure A3). Forty studies monitored nest boxes over 3 years and 37 more monitored them over 4+ years, including one documenting change in nest box colonizers over 17-years in Mexico (Roubik & Villanueva-Gutierrez, 2009), and another monitored *O. rufa* (Linnaeus) off and on over 27 years in Ukraine (Ivanov, 2006) (Figure A3). Studies that use nest boxes have occurred around the world but the majority of published research has occurred in the United States, Europe, and South America (especially Brazil) (Appendix C).

. More publications using nest boxes investigate cavity-nesting bees only (67% of total) compared only wasps (15%) or both (18%). Among these, mason bees [*Osmia* spp.; especially *O. lignaria* Say in North America, and *O. rufa* and *O. cornuta* (Latrielle) in Europe] and leaf-cutting bees (*Megachile*: Megachilidae) were the most studied. In general though, nest boxes attract both bees and wasps but placement and size affects which species colonize. For example, wasps occur more often in nest boxes in partial or full shade, including those set up in forests (Taki et al. 2008a; Buschini & Woiski, 2008). Some bees are gregarious like *O. bicornis* (Seidelmann, 2006) or *M. rotundata* (Fabricius) (Pitts-Singer & Cane, 2011) and tend to abundantly colonize nest blocks containing hundreds of nesting holes

4.1. Motivation

Diversity

Of the 360 studies, 69 (18%) focused on local species diversity (Table A1). Of these, an overwhelming proportion (66.7%) examined bees and wasps together (47 of 69), 27.8% (18) bees only and 5.5% (4) wasps only. Bee diversity studies varied in spatial scale across specific habitat types (Moroń et al. 2008; Westphal et al. 2008; Sobek et al. 2009; Diekötter et al. 2014), or in the presence or absence of nest site availability or foraging resources (Fabian et al. 2014). The success of habitat restoration efforts has been measured using nest box colonization and species diversity. For example Moron et al. (2012) studied diversity across a gradient of metal contamination and Beyer (1987) examined wasp diversity near and far from fluoride emission sites. In these applications, nest boxes are more useful than sampling with nets or pans because they provide greater detail on where the species is living, rather than just habitat where they may be passing through (e.g. Grixti & Packer, 2006).

Interactions at a nest box between co-occurring bee and wasp species are well studied (N=24), for example the supersedure of different species competing for nest sites (Delphia &

O'Neill, 2012). Supersedure in nest boxes results when a nest built by an early active species is built over by a late season species. This can doom the earlier species now unable to emerge and could be problematic for conservation or enhancement of some species (Bohart, 1955). Others examined the impacts of more complex multitrophic interactions among bees and wasps, floral and prey preferences, and parasites (N=27). Acknowledging the diversity of species and interactions at nest boxes, not just the rate of colonization can help elucidate the relative benefit to target taxa, for example, native bee species. Aggregating co-occurring bee, wasp, and parasite species in nest boxes however, could have negative impacts on population dynamics, by facilitating the building up of introduced species (e.g. *M. apicalis* Spinola: Barthell et al. 1998), natural enemies (Freeman & Jayasingh, 1975; Wcislo, 1996), or attacks by birds or other wildlife (Krunic et al. 2005). These negative impacts warrant further study as artificial habitat preferred by aggressive or competitive species or providing predators easier access might have negative consequences for local bee and wasp communities.

Design

Twenty-three studies (7% of total) assessed the impact of nest box design on use by bees, predominantly on attractiveness to bees having potential as managed pollinators (Kim, 1992; Bosch & Kemp, 2002) (Table A1). This work is motivated by improving orientation of bees to their nests (Guédot et al. 2005) and efficiencies in offspring production (Levin, 1957; Stephen, 1961; Artz et al. 2014). Only one study examined features intended for both bees and wasps by bundling bamboo stalks in different arrangements, with no evident 'best arrangement' (Matsumoto & Makino, 2011). One other found adding shading structures atop nest boxes preferentially attracts wasps in forest fragments (Taki et al. 2008b).

Patterning and colouration of the area around the nest box entrance can improve orientation to home nesting tubes in nest boxes containing multiple tubes (Krombein, 1967; Lee-

Mäder et al. 2010). For example, visual cues at the entrance to nest sites improved locating of home nesting holes in *O. cornuta* and *O. lignaria* (Fauria & Campan, 1998), and *M. rotundata* (Fauria et al. 2004). Colour can also impact offspring production: Artz et al. (2014) found that *O. lignaria* provisioned 1.4 and 2.6 times more females in nest boxes that were light blue compared to orange and yellow coloured nest boxes because they were more easy to locate. However, excess patterning can confuse bees at the nest entrance. Guédot et al. (2007) found increasing disorientation at nests with increasing three-dimensionality and excessive colouring. Disorientation could extend return foraging bouts, reducing the time dedicated to provisioning offspring and nest building.

The positioning of a nest box impacts the type and number of colonizers (Gaston et al. 2005). Everaars et al. (2011) handed out numerous nest boxes to citizens of Leipzig, Germany to monitor populations of *O. bicornis* (Linnaeus) and found the hang location was a significant influence on presence of the bee (balconies, carports > trees, shrubs). Nest boxes are also less colonized if facing prevailing winds (Martins et al. 2012) and with increasing height from ground level on vegetated roof tops (MacIvor, 2015).

Design of nest boxes could also be motivated by ease of maintenance to minimize parasites, pathogens, and diseases that can accumulate (Hobbs, 1968; James, 2005). In a review, Wcislo (1996) found larvae in nest boxes had higher rates of parasitism than those in naturally occurring plant stems. Although cleptoparasites of bees are useful bioindicators of local habitat quality (Sheffield et al. 2013), design that reduces their impacts on pollinators is important for agricultural productivity, public interest in building and purchasing nest boxes, and the relevance of nest boxes as tools in nest building bee and wasp conservation (MacIvor & Packer, 2015).

Pollination enhancement

Literature on the topic of enhancing numbers of nest box colonizers (13% of all studies examined) has focused almost solely on best management practices to enhance bees for pollination services (20 of 21 studies). Mason bees (*Osmia*: Megachilidae) are among those that have received the most attention: Bosch & Kemp (2002) review the conditions needed to develop *Osmia spp.* as effective crop pollinators, including rearing and release methods, densities of bees needed to ensure adequate and reliable pollination rates, nesting materials used, as well as control of parasites and pathogens. Sedivy & Dorn (2014) cover the management of *Osmia* spp. specifically as pollinators of fruit trees. Krunic et al. (2005) examines the accompanying fauna of *Osmia* spp. in nest boxes, their brood parasites, and vagrant species occupying nesting holes meant for bees. Others review nest site selection and nesting materials. For example, Cane et al. (2007) provide an overview of the nesting substrates used by the North American *Osmia* spp., and Morato & Martins (2006) reviews the factors affecting bees and wasps nesting in wood and their implications for nest box design.

Local and landscape

Only 13% of studies examined landscape factors impacting colonization of nest boxes. Of these, 17 were interested in both bees and wasps, 14 examined bees only and 4 others examined wasps only. These occurred in a variety of habitat types, but agricultural landscapes and impacts of proximity to and size of hedgerows, buffer strips, forest patches, and other nearby habitat within an agricultural matrix was the most studied (Steffan-Dewenter, 2002). For example, Holzschuh et al. (2009) determined that caterpillar-collecting wasp colonization was between 2.7-6 times higher in agroecosystems when grass strips were connected to forest edges.

Nest boxes have been used to examine the effects of fragmentation on bee and wasp populations in numerous managed landscapes (Klein et al. 2006; Krewenka et al. 2011;

Coudrain et al. 2014). In general, increasing distance from nest materials and forage plants has been shown to have a negative impact on cavity-nesting bee diversity and reproductive success. Jauker et al. (2012) demonstrated declining nest box colonization with increasing scarcity of semi-natural grasslands in a large agricultural matrix. However, Schüepp et al. (2011) found that isolation from forest fragments in an agroecosystem reduced diversity of natural enemies more strongly than colonizing bees and wasps. With higher resolution mapping increasingly available for analyzing landscape variables (e.g. Zhou et al. 2009) continued study of bees, wasps, and parasite using nest boxes is expected to yield important details about habitat quality (Tscharntke et al. 1998) and multitrophic stability (Laliberte & Tylianakis, 2010).

Nesting biology

Nesting biology of bees and wasps constituted 41% of investigations (Table A1). These include those that have examined incubation and overwintering conditions (e.g. Tepedino & Parker, 1986; Kemp & Bosch, 2001; Giejdasz & Wilkaniec, 2002; Yocum et al. 2005; O'Neill et al. 2011; Fliszkiewick et al. 2012; Fründ et al. 2013), sex ratio (e.g. Tepedino, 1980; Longair, 1981; Oku & Nishida, 1999; Seidelmann et al. 2010; Nascimento & Garofalo, 2014), embryonic (Torchio, 1989) and larval instar development (Whitfield et al. 1987), metabolic rates (Sgolastra et al. 2012), changes in egg size (Maeta & Suguira, 1990), cocoon size (Tepedino & Parker, 1986) and orientation (Torchio, 1980; Martins et al. 2012), diet (Sedivy et al. 2011; Haider et al. 2013), nest building materials (Horne, 1995), nest site fidelity (Steffan-Dewenter & Schiele, 2004) and emergence and seasonality (Thiele, 2005; Forrest & Thomson, 2011).

Research on these topics was predominantly focused on bees (89 of 136 studies). Most researchers were interested in the study of a single species (e.g. Jaycox, 1967; Frohlich & Parker, 1983; Boesi et al. 2005; Zajdel et al. 2014) and these investigations have led to successful management of different pollinators including *O. cornifrons* (Radoszkowski) (Maeta &

Kitamura, 1974), *O. lignaria* (Bohart, 1972; Philips & Klostermeyer, 1978), *O. cornuta* (Bosch & Kemp, 2002), and *M. rotundata* (Bohart, 1972; Fairey et al. 1984; Pitts-Singer & Cane, 2011). Another seven studies examined the nesting biology of both bees and wasps, and 40 total examined the nesting biology of wasps only.

Foraging

Understanding the type and quality of foraging resources available, as well as the efficiency and distances travelled by bees or wasps seeking food or nesting resources, should inform the number and placement of nest boxes. Such work represented 24% of all examined in this review. Nest boxes are used to estimate the time spent foraging or the minimum and maximum foraging distances travelled (Klostermeyer & Gerber, 1969). Gathmann & Tscharntke (2002) investigated foraging distances of 16 bee species and found rather short foraging ranges that increased with bee size extending no more than 600m from a nest box. Greenleaf et al. (2007) suggested foraging distances ranged from 150-700m and increased with increasing bee size, but Zurbuchen et al. (2010a) found maximum flight distances are considerably shorter, and within dozens of meters for some small species. Manipulative experiments can be conducted using nest boxes positioned at distances from foraging resources or across barriers to investigate impacts on foraging effort. Peterson & Roitberg (2006) found decreases in resources allocated to offspring in *M. rotundata* when nest boxes were set further distances from a large forage resource. Krewenka et al. (2011) examined hedgerows, roads and other potential barriers to cavity-nesting bees and wasps and found no impact on foraging efficacy.

Those interested in bee foraging ecology focus on the type and diversity of pollen collected to examine floral preferences. In palynological analyses, pollen fresh from the bodies of foraging bees or from frass obtained from brood cells is used (Williams & Tepedino, 2003; De Lyra Neves et al. 2014; Eckhardt et al. 2014; MacIvor et al. 2014). Others have used nest boxes

to quantify nectar resources (Burkle & Irwin, 2009; Cane et al. 2011). Mark recapture methods are used to examine nest site fidelity and population size of different bee taxa (Steffan-Dewenter & Schiele, 2004; Zurbuchen et al. 2010b; Yamamoto et al. 2014).

The type and diversity of prey collected by different wasp populations can also be readily assessed. Prey diversity has been examined among beetle and caterpillar-feeding *Symmorphus* wasps (Family: Vespidae) (Sears et al. 2001; Budriene, 2003), spider-collecting *Trypoxylon* (Family: Crabronidae) (Matthews and Matthews, 1968; Buschini et al. 2010; Coudrain et al. 2013) and *Dipogon* (Crabronidae) (Jennings & Parker, 1987), aphid-collecting *Passaloecus* (Crabronidae) (Fricke, 1993), and katydid-collecting *Isodontia mexicana* (Family: Sphecidae) (O'Neill & O'Neill, 2003; Ercit, 2014).

Toxicology

Only 4% examine questions pertaining to toxicological impacts of pesticide or insecticide applications on bees using nest boxes (none investigate wasps). These chemicals are applied to flower-bearing crops and horticultural plants that are visited by bees (Torchio, 1983; Alston et al. 2007).

The impacts of pesticides and herbicides have been studied predominantly on honey bees (Oldroyd, 2007; Henry et al. 2012) and bumble bees (Whitehorn et al. 2012). However, cavity-nesting bees are excellent models for understanding how these chemicals impact wild bees and pollination services more generally (Brittain & Potts, 2011). Since nest boxes can be set up in different habitats, manipulated spatially and temporally, and house numerous species, they could be extraordinarily useful tools to monitor impacts of pesticide and insecticide applications (Sekita & Yamada, 1993; Alston et al. 2007).

Nest boxes can be used to collect bees and wasp larvae for toxicological study. Konrad et al. (2008) fed transgenic crop pollen with insecticidal protein additives to *O. bicornis* larvae in

nest boxes in greenhouse enclosures and noted negative impacts on survival. Further, Sandrock et al. (2014) found neonicotinoid-based insecticides had a significant impact in reducing reproductive success in *O. bicornis* obtained from nest boxes. Nest boxes also permit study of other potential vectors of pesticide uptake by bees including nesting materials. Waller (1969) found insecticides sprayed on alfalfa leaves used by *M. rotundata* as nest building resulted in 100% mortality of larvae. Given the ease of set up and monitoring of nest boxes, researchers might also find predatory wasps useful bioindicators of concentrations of these chemicals to evaluate effects in more complex food webs and further up the food chain (e.g. spider collecting wasps).

4.2. Nestbox material

Materials vary widely and have for the last century. In Cambridge, UK, Balfour-Browne (1925)'s 'bee wall' used bricks to hold elderberry stems and glass tubes in place to survey local cavity-nesting bee and wasp populations in a residential garden. Since, numerous other nesting tube materials have been tried, with mixed success. In general, the nesting tube elements of a nest box can be delineated into four main types: 1) Bamboo, reeds, and pith-bearing stems, 2) Drill holes in wood, 3) Cylindrically rolled paper or cardboard tubes, and 4) artificial materials such as glass, polystyrene or other plastic (Figure A1).

Bamboo, reeds, pith-bearing stems

Bamboo, reeds, other stems having pith, and hollow sticks were used in more than a third of all studies (39.5%) (Figure A1A-B). Hicks (1937) described collecting stems from pith-bearing plants including sumac, blackberry, raspberry, rose, elderberry, mullein, and various others. These range considerably in diameter (2 to 10 or 20mm as in Gathmann et al. 1994; Tscharntke et al. 1998; Coudrain et al. 2013) (Figure A4), and are collected, dried, and bundled together,

often enclosed in waterproofing structures.

The word ‘Bamboo’ is used often (N=47) to describe nesting tubes of bamboo origins (Figure A1A). Three bamboo species were named *Phyllostachys aurea* Riviere & C. Riviere (Poacaeae) (N=1) (Musicante and Salvo, 2010), *Arundo donax* L. (Poaceae) (N=7), and *Fallopia japonica* (Houtt.) Ronse Decr. (Polygonaceae) (N=3) (Table A2). ‘Reed’ is also used to describe the nesting material used (N=10), however the dominant reed identified was *Phragmites australis* (Cav.) Trin. ex Steud. (N=44) with one other reed species listed: *Saccharum spontaneum* L. (Poaceae) (Kessler et al. 2009). Bamboo and reeds are sometimes fitted with a rolled paper insert so the colonizers are easily removed (2.8% of total). Among pith-bearing stems and branches, the most commonly used were elderberry (*Sambucus*: Adoxaceae) (N=20) (Cane et al. 2007) and raspberry and blackberry (*Rubus*: Rosaceae) (N=6) (e.g. Danks, 1971) (Table A2). Opening bamboo, reeds, and stems to observe nesting activity often requires their destruction, however Frohlich (1983) describes a setup where *Sambucus* sp. canes were split longitudinally, lined up, and overlaid with a glass plate for observation.

Drill holes in wood

Wooden nest boxes were used most often, representing 48.3% of all studies. Among these, two main designs were common. The first consists of any number of holes drilled (can vary in diameter) into a solid block of wood (Figure A1C-D); these are easily fabricated with even the most basic tools and materials. However, because these are difficult to open, they are difficult to clean, which reduces their usefulness year-over-year (Lee-Mäder et al. 2010). Many wooden nest boxes include rolled paper cylinders placed inside each drilled nesting hole (15% of total). This permits the investigator to easily remove and replace the tubes to ensure nesting tubes are available all season to accommodate species with different flight periods. When paper rolls are not inserted, some nesting materials (e.g. tree resins and sap) are nearly impossible to remove.

In general, studies using drill holes in wood have to allow all individuals to emerge through the front entrance to permit identification. Drilled wood nest boxes can be placed in mesh bags, or vials can be attached to catch all emerging colonizers (Roubik & Villanueva-Gutiérrez, 2009; Forrest & Thomson, 2011).

A second, more refined design type has emerged: these are made of a series of identically sized thin wood planks all with bore holes drilled along one exposed side (Figure A1E-F). The planks are bundled in series so that holes on each plank are fit tightly against the non-bored side of the adjacent plank. Krombein (1967) added paraffin wax around the edges of ill-fitting nesting planks creating both a waterproof seal and parasite blocker. These create a series of enclosed nesting holes that can be opened and kept clean (Fricke, 1991b; Hallett, 2001; Cane et al. 2011). More recent designs have used other materials to improve the seal between wooden boards, including thin layers of foam and clear acetate sheets to view brood development and other within-nest processes (e.g. Hallett, 2001).

Authors using wooden nest boxes find them to be more attractive to bees than other nest box material, including vermiculite (Martins et al. 2012) and polystyrene (Torchio et al. 1984), but rarely is the type or species of wood used specified. Pine (*Pinus*: Pinaceae) was the most common wood identified (N=22). Others included Fir (*Abies*: Pinaceae) (Coville & Griswold, 1984), Spruce (*Picea*: Pinaceae) (Chapman & Stewart, 1996), Aspen (*Populus*: Salicaceae) (Peck & Bolton, 1946), Cedar (*Thuja*: Pinaceae) (Jennings & Parker, 1987), Oak (*Quercus lobata*: Fagaceae) (Barthell et al. 1998), and Redwood (e.g. Torchio, 1981).

Cylindrically rolled paper or cardboard tubes

Rolled paper tubes or fabricated ones made of cardboard are also bundled together without setting them into wood bore holes or bamboo (11.7% of total) (Stubbs et al. 1994; Taki et al. 2004; MacIvor & Packer, 2015). The thickness of the tube can impact the number of parasites

attacking, with thinner walled nesting tubes being more easily punctured by ovipositors of some brood parasites, such as *Monodontomerus* (Torymidae) (Stephen & Every, 1970). These nests are often bundled into weather protective boxes, including milk cartons (e.g. Sheffield et al. 2008a), PVC piping (e.g. Diekötter et al. 2014; MacIvor et al. 2014) (Figure A1G), or wooden boxes (e.g. Everaars et al. 2011).

Paper and cardboard tubes can be custom fabricated and purchased for precise and consistent nesting tube diameters (e.g. Abel & Wilson, 1998; O'Neill & O'Neill, 2010). Some are designed for easy opening to record the contents and to remove larvae for further study or incubation (MacIvor & Moore, 2013). These nesting tubes, due to their availability, low cost and precision in dimensionality (to target species with particular hole diameter preferences), are useful for research but extra work to open, replace and maintain. As a result these are rarely used in agriculture where large numbers of nests and minimal maintenance are desired.

Artificial materials - Glass

Glass tubes were adopted early on in the use of nest boxes as tools in research because they permit viewing of nest building behaviour (Balfour-Browne, 1925; Frost, 1943). Some species appear to use glass tubes readily: Taylor (1922) made observations on the nesting biology of *Ancistrocerus* (Vespidae) wasps using glass tubes and Hartman (1944) made similar notes on the nests of the mason bee *Osmia georgica*. Others detail the nest building behaviour and development of *Megachile pugnata* Say (Frohlich & Parker, 1983), and *M. rotundata* and *M. apicalis* (Trostle & Torchio, 1994) in glass tubes. However only 1.1% of all studies used glass tubes and no studies have used them in more than two decades. Decline in the use of glass tubes to study nesting biology resulted from observations indicating excessive growth of mold that impacts mortality (Medler & Fye, 1956). Greenburg (1982) used a topical treatment of Tegosept, for mold that developed on the surface of managed ground nesting *Lasioglossum*

zephyrum (Smith) (Hymenoptera: Halictidae). Similar treatments might be useful to mitigate mold development in nest boxes.

Artificial materials - Plastic tubes

Plastic tubes have been used infrequently and include plastic drinking straws (Stephen, 1961; Gerber & Klostermeyer, 1970; Sekita & Yamada, 1993), rubber tubing (Medler, 1965), and corrugated plastic sheets (Stephen & Every, 1970) (1.7% of all studies). However, plastics have been shown to impede the success of colonizing bees and wasps. Fye (1965) lists several reasons for this, including the 'attractiveness to and destruction by bears' (Stephen, 1961), but more importantly because water cannot diffuse through plastic, (or glass) and brood is more likely to succumb to mold as a result. Repeated work with plastic straws by Stephen & Every (1970) showed up to 90% mortality in *M. rotundata* due to mold. Few researchers use plastic based nesting tubes now because of this issue and the availability of other natural materials.

Artificial materials - Polystyrene boards

Polystyrene-based nesting boards were used in 5.8% of studies (Figure A1H). These can support large populations of solitary bees and have been developed for managing solitary bees for agriculture (Kemp & Bosch, 2001). Richards (1978) found polystyrene to support higher numbers of viable offspring than other nest box materials including paper and cardboard tubes, and drilled particleboard. Due to their large size, polystyrene boards can be useful for studies requiring large numbers of individual nests (Rothschild, 1979; Radmacher & Strohm, 2010; 2011).

4.3. Nesting tube diameter and length

Nesting tube diameters and lengths can vary widely but depend on the taxa under investigation

(Fye, 1965; Krombein, 1967; Fricke, 1991a). Among the studies that explicitly report the nesting tube diameter(s) used (N=271 of 360 studies), these ranged from as narrow as 1mm (e.g. Tormos et al. 2005; Fernandez-Triana et al. 2005) to as wide as 25mm (e.g. Camillo, 2005; Kessler et al. 2009). Colonizers generally prefer diameters that best match their body width. For example, studies interested in small aphid-collecting wasps (*Passaloecus* or *Psenulus* spp.) use diameters between 1-4mm (Fricke, 1993), whereas those on medium-sized bees in (*Megachile* or *Osmia* spp.) use diameters between 5-8mm Bosch and Kemp (2002). The best nesting tube widths for *Hylaeus* spp. (Colletidae) is less clear as these bees nest with cells across the diameter in the tube (Torchio, 1984).

Surveys interested in species diversity often deploy nest boxes that contain multiple nesting tube widths. These ranged in number per nest box from 1-8 for those using paper or wood based devices (Figure A4). Bamboo or reeds have natural variation in stem diameter (Tscharntke et al. 1998) rarely in studies were these accounted for between nest tubes within and across nest boxes. Nesting tube diameter can influence bee and wasp sex ratios, such that diameters too small result in higher numbers of male offspring (Stephen & Osgood, 1965; Krombein, 1967; Rothschild, 1979; Longair, 1981). This is due to a sexual dimorphism in body size where females are larger than males, except in Anthiidine species (Stubblefield & Seger, 1994). Apart from these motivations, when a single bee or wasp species was the focus, a single nesting tube diameter was used in all cases (Figure A4).

Nesting tube lengths are generally 150mm but range up to 200-300mm, and sometimes are much shorter. For example, 50mm in Paini (2004), 58-85mm in Gazola & Garófalo (2003), 70mm in Zillikens & Steiner (2004), 75mm in Wilson & Holway (2010), 100mm in Kuhn & Ambrose (1984) and 115mm in Vinson et al. (2010). Lengths shorter than 150mm have been linked to increases in male production (Gerber & Klostermeyer, 1970; Gruber et al. 2011), but others have found no effect (Jay & Mohr, 1987). Seidelmann (2006) attributes the bias to

females provisioning less costly offspring (e.g. males) nearer the nest entrance where the risk of parasitism is highest; the shorter the tube, the shorter the minimum distance to the entrance.

4.4. Habitat types

Six main habitat types were identified from the literature. Some studies examined several kinds of habitats ('various': 19% of total) to examine how different areas or management regimes (e.g. along a gradient of urbanization from natural to agricultural to urban) impact species of interest (Buschini & Fajardo, 2010; Schüepp et al. 2011) or food web dynamics (Tylianakis et al. 2007).

Agriculture

Agricultural landscapes, including those identified as agroecosystems or orchards, were the most commonly surveyed (28% of total) (Table A3). Pollination services provided by bees were of predominant interest (80% of studies on bees only) (Bohart, 1972). Cavity-nesting bees have been studied using nest boxes in a multitude of crop types, including alfalfa (Wrightman & Rogers, 1978; Bosch & Kemp, 2005), carrot (Tepedino & Frohlich, 1984), onion (Giejdasz et al. 2005), rapeseed (Teper & Bilinski, 2009), coffee (Laliberte & Tylianakis, 2010), almond (Torchio et al. 1981; Bosch, 1994), blueberry (Stubbs et al. 1997; Sampson et al. 2004), cherry (Bosch et al. 2006), prune (Torchio, 1976) acerola (Pina & Aguiar, 2011; Magalhaes & Freitas, 2013), apple (Wei et al. 2002; Sheffield et al. 2008b; Gruber et al. 2011), and passion fruit (Junqueira et al. 2012; Yamamoto et al. 2014). Multi-crop systems have been shown to harbor a greater diversity of cavity-nesting bees and wasps in nest boxes compared to monocrop systems (Banos-Picon et al. 2013). Fields containing other economically important plants have been surveyed too; for example, O'Neill et al. (2010) studied feral populations of *M. rotundata* at a wildflower seed farm.

Other topics covered in agricultural areas include bee larval development and

overwintering success (O'Neill et al. 2011), and defense against parasites (Cusumano et al. 2012) and pathogens (Goettel et al. 1997). The potential for nest box managed wasps to contribute to pest regulating services has been underrepresented and is an opportunity for research and application impacting crop protection and stability.

Open Habitat

Open habitats (18%) were broadly classified to include all natural areas not enclosed by forest, converted to agriculture, or experiencing urbanization. These included open fields, grasslands, old pastures and meadows (N=48), deserts (N=4), mountainous areas (N=5), and marshes and wetlands (N=4). In this broad category of non-cultivated, non-forest, non-urban habitat, bees alone were surveyed 69% of the time, 11% investigated both bees and wasps, and 20% were concerned only with wasp taxa. Work in these habitats was primarily motivated by questions regarding environmental variables and their impact on species diversity. These habitats also generally provided grounds for work on plant pollinator interactions (Dorado et al. 2011), palynology (Levin & Haydak, 1957; Raw, 1974; Williams, 2003), interactions with parasites (Münster- Swendsen & Calabuig 2000; Kruess & Tscharntke, 2002) and other multi-species interactions. For example, Forrest & Thomson (2011) examined synchrony in flowering times and bee emergence using individuals collected in nest boxes set out in different mountainous meadow habitats.

Forests

Forest habitats were those under tree canopy where shade by trees might influence the types of bees and wasps visiting (17% of studies, N=60) (Table A3). Compared to other habitat types, wasps were surveyed in forests more often (30% of the time). Only 37% examined bees only (e.g. Thiele, 2005; Gazola & Garófalo, 2009), and 33% examined both bees and wasps (e.g.

Aguiar et al. 2004; Sobek et al. 2009). Wasps tend to nest more frequently in shaded nest boxes compared to bees, as occurring in closed canopy habitat (Taki et al. 2004). Moreover prey items of different wasps, including spiders and caterpillars are found in forests and forest edges (Jennings & Parker, 1987; Budrienė, 2003).

Nest boxes set up in forests included forest edges (Holzschuh et al. 2009), fragments (Tylianakis et al. 2006; Roubik & Villanueva-Gutierrez, 2009), and in large forest reserves (Kamke et al. 2008; O'Neill & O'Neill, 2009; 2013). Many studies occurring in forests were carried out in South America (55% of total from forests).

Campuses, Botanical Gardens

University campuses and botanical gardens where flora is managed were surveyed in 6% (N=21) of the data (Table A3). Bees were the focus in 76% of these studies, both bees and wasps in 5%, and 19% were interested in wasps only. University campuses often contain diverse and well-maintained plantings that are accessible, and close to research facilities. Research in these areas are often small in scale, consisting of a single large nest box or several set up at sites that can be monitored daily. These cover different aspects of nesting biology (Fricke, 1992; Zanette et al. 2004) and behaviour of select species and their parasites (Gazola & Garofalo, 2003). For example, from observations of nest boxes set up at a University maintained forest understory, Rocha-Filho et al. (2009) recorded a new host record for *Aglaomelissa duckei* on *Centris analis*.

Botanical gardens usually have even more well-maintained landscapes, and are rich in flowering vegetation. Because of the diversity of flowers at botanical gardens, Dobson et al. (2012) was able to cultivate and use more than 15 flower species to examine imprinting of larval food on flower choice as adults in *O. bicornis*, but found no evidence.

Urban

Urban areas where heterogeneity in habitat is high as a result of diverse private landscape management were surveyed in 5% of publications examined (N=19). Of these, 63% were focused on bees only, 21% on both bees and wasps, and 16% on wasps only. Urbanization creates conditions that have strong negative impacts on some bee species, while others are seemingly unaffected (Banaszak-Cibicka & Żmihorski, 2012; Baldock et al. 2015). These trends are readily assessed using nest boxes set up across large urban areas (Everaars et al. 2011). Nest boxes can also be used to survey changes in diversity and abundance within and between different urban green space types (Gaston et al. 2005; MacIvor & Packer, 2015).

Cities contain large numbers of residential dwellings with adjacent green space that is privately managed (Feagan & Ripmeester, 1999; Davies et al. 2008). Nest boxes in these environments not only monitor impacts of small-scale landscape manipulation (e.g. gardening) on bee and wasp populations, but also engage citizens in in bee and wasp diversity and significance for pollination and pest control in urban agriculture.

Enclosures

Six percent (N=25) used bees purchased or collected from the field for experimentation in enclosures, including in greenhouses, flight cages and other laboratory settings (Table A3). In enclosures, including flight cages, green houses, and growth chambers, numbers and diversity of bees, and floral and nesting elements can be controlled. Research using enclosures is dependent on a working knowledge of the species' reproductive, nesting, and foraging requirements. As a result, these studies examine basic questions in ecology and behaviour of specific species, for example, floral preference of *O. cornifrons* (Abel & Wilson, 1988), leaf choice by the leaf cutting bee, *M. rotundata* (Horne, 1995) nest-building activity of *O. bruneri* Cockerell (Frohlich, 1983), brood parasitism of *O. pumila* (Goodell, 2003), or parental investment

and sex ratios in *O. cornifrons* (Saguira & Maeta, 1989). By manipulating the diversity of bees 'seeded' into nest boxes in flight cages, Fründ et al. (2013) showed additive impacts of bee diversity, and especially functional complementarity among bee species, on higher seed production.

5. Research Opportunities

Investigation of multi-trophic interactions

The relationships between bees and wasps and the relative and combinative influences of their parasites, competitors for nesting locations, and resources require more ecological network analysis: there have been few such studies (Albrecht et al. 2007; Ebeling et al. 2012; Fabian et al. 2013). Fabian et al. (2013) examined how landscape structure impacted hymenopteran food webs and found more links between species and higher diversity of interactions in more heterogenous agroecosystems that had higher proportions of forest cover. Using nest boxes set up in a coffee agroecosystem, Veddeler et al. (2010) found that temporal variability in parasitism decreased with parasite diversity in cavity-nesting wasps but not bees. Additional work that empirically assesses change in multitrophic interactions between cavity-nesters and the foraging and nesting material they collect can inform planning for cavity-nesters and the complexity of their needs.

Detailed analysis of nesting material constituents

Studies that examine the identity and availability of nesting materials are few. For example, Horne (1995) examined the preference of *M. rotundata* for 11 plant species for nest material, finding buckwheat and alfalfa as favourites and no effect of leaf toughness on choice. Cane et al. (2007) reviewed different substrates and materials used by *Osmia* spp. in North America. Aside from these two, most list nest material identities by superficial designations of mud, rolled

leaves, masticated leaves, resin, etc. These data could be extremely useful for agroecosystem planning to ensure these resources are abundantly available to enhance wild pollinator abundance. Many sources of nesting materials are flowers, shrubs and trees, and their identification (e.g. through DNA barcoding) as nesting material for native bees could also result in their inclusion in streetscapes or residential gardens to include more than just flowers in urban pollinator conservation planning.

Monitor human impacts in cultivated crop systems

Nest boxes can be used to study human impacts on native wild bee populations. For example, Paini and Roberts (2005) found nest construction in the cavity-nester *Hylaeus alcyoneus* Erichson declined by 23% in sites with honey bee hives nearby compared to control sites. Nest boxes set up at distances away from honey bee colonies could be used to determine densities of honey bee hives so not to impact wild bee populations or to minimize competition in overlapping management of both honey bees and wild bees for crop pollination.

Nest boxes can also be set up at distances away from treated crops to elucidate impacts of proximity to application. Because they can be easily opened, the nests can be dissected at different points in a year to assess nest development, fecundity, and concentrations of chemicals. Further the impacts on foraging behaviour can be quantified by examining activity at the nest entrance over the season. Lastly, nest boxes can be used to gather larvae for emergence and further testing in laboratory experiments or flight cages to limit environmental factors that influence results in the field.

Manipulation of nestbox colonizers within or between seasons

Using nest boxes in manipulation studies is not common, but these devices provide excellent models to elucidate causation among ecological observations. For example, the type and

number of nest boxes, nest tubes, and bees, wasps, and parasites can all be adjusted to address different research questions. As well, colonizers from nest boxes can be used in experiments that manipulate their diets (Williams, 2003; Praz et al. 2008), their developmental conditions (Tepedino & Parker, 1986), or their environment post emergence in flight cages (Goodell, 2003). Junquiera et al. (2012) investigated the potential of *Xylocopa frontalis* (Olivier) and *X. grisescens* Lepeletier as managed pollinators of passion fruit by 'seeding' bees into nest boxes. 'Seeding' bees into nest boxes could help establish populations in agriculture (e.g. Williams & Kremen, 2007) for applications in pollinator management, as well as to evaluate numerous local (e.g. novel competitors) and landscape effects (change in environmental conditions, e.g. distance to resources) on population dynamics.

Nestboxes as tools in citizen science

Significant interest is growing among the public in participating in broad scale research, and scientists are increasingly aware of the potential opportunities in harnessing citizen scientists to aid in data collection and observation (Silvertown, 2009). Because nest boxes can be inexpensive, small, and lightweight, they can be given out to interested property owners for sampling, resulting in hundreds (or, thousands) of survey sites over large geographic areas (Everaars et al. 2011; MacIvor et al. 2014). With online resources to disseminate findings from nest boxes, these could be useful tools to not only collect meaningful ecological data but also engage citizens with pollinators, their diversity, and considerations for enhancing habitat. Nest boxes can be used to introduce people to the fact that wild bees are diverse and there are more than just honey bees. Since the density of bees and wasps is much lower in nest boxes than in honey bee colonies, nest boxes could be used to help people overcome their fear of bees for risk of being stung. Nest boxes might also be considered in landscape architecture, urban planning and design for pollinators where as designed experiments (e.g. Felson & Pickett, 2005)

could inform new applications in these multidisciplinary fields.

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7. Tables

Table A1. Motivations for research of cavity-nesting bees and wasps using nestboxes (N=360).

Motivation	Application	% of studies
Diversity	Monitoring bee and wasp assemblages	18%
Design	Material, dimension, placement	7%
Pollination	Increase the numbers of bees to enhance pollination services	13%
Landscape	Correlating local and landscape variables with nest box colonizers	13%
Nesting	Behavior and ecology of bees and wasps at the nest site	41%
Foraging	Understanding the type, quality, and efficiency of bees or wasps foraging for food or nesting material	24%
Toxicology	Insecticides, pesticides impacts on wild bees	4%

Table A2. List of bamboo, reed, and plant stem species used successfully as nesting tubes.

Species	Family	Common Name	Type	No. Studies
'Bamboo'	-	'Bamboo'	Bamboo	47
Phyllostachys aurea Riviere & C.Riviere	Poaceae	Golden Bamboo	Bamboo	1
Arundo donax L.	Poaceae	Giant Cane	Bamboo	8
Fallopia japonica (Houtt.) Ronse Decr.	Polygonaceae	Japanese knotweed	Bamboo	3
Ricinis communis	Euphorbiaceae	Castor	Bamboo	1
'Reed'	-	'Reed'	Reed	10
Phragmites australis (Cav.) Trin. ex Steud.	Poaceae	Common Reed	Reed	44
Saccharum spontaneum	Poaceae	Kans grass	Reed	1
Xanthorrhoea minor R.Br.	Xanthorrhoeaceae	Grasstree	Stem	2
Sambucus sp.	Adoxaceae	Elderberry	Stick	18
Rubus fructicosus L. sens.str.	Rosaceae	Blackberry	Stick	1
Rubus strigosus Michx.	Rosaceae	Raspberry	Stick	3
Erythrina poeppigiana (Walp.) O.F. Cook	Fabaceae	Dadap	Stick	1
Melia azedarach L.	Meliaceae	Chinaberry	Stick	1
Conium maculatum L.		Poison Hemlock	Stick	
Ailanthus altissima (Mill.) Swingle	Simaroubaceae	Tree of Heaven	Stick	1
Rhus typhina L.	Anacardiaceae	Sumac	Stick	1
Dipteryx alata Vogel	Fabaceae	Baru Tree	Stick	1

Table A3. Habitat types surveyed. ‘Various’ category denotes studies that use multiple sites types or region.

Study Location	% of studies
Agriculture, Agroecosystems, Orchards	28%
Enclosures: Cage, Greenhouse, Lab	7%
Campus, Botanical Gardens	6%
Forest	17%
Open	18%
Urban	5%
Various	19%

8. Figures

Figure A1. Different nest box designs developed for research and outreach. A. *Hylaeus* sp. emerging from bamboo cane (Photo: Rob Cruickshank), B. A nest box made of cut bamboo internodes for sale, C. Nesting log installed at Toronto Botanical Gardens, D. Wood blocks with drill holes colonized by different bee and wasp species, E. Wooden boards drilled down one side and bundled (Photo: Peter Hallett), F. Inside of a wood plank with drill holes down one side to view nest construction (Photo: Sarah Peebles), G. Extruded polystyrene blocks inserted into a wooden frame, H. cardboard paper tubes inserted into insulation board fit into PVC piping.

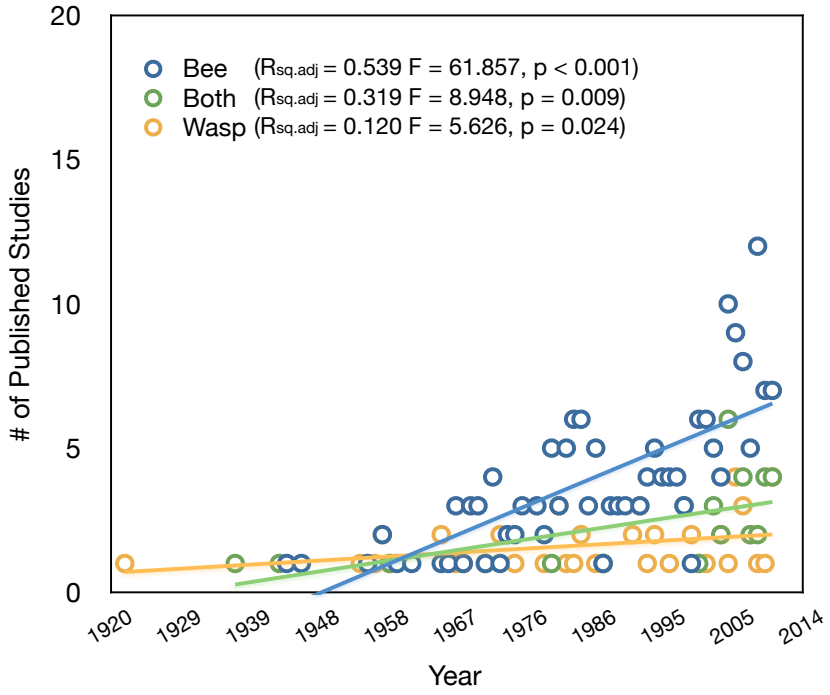


Figure A2. The number of studies on bees, wasps, or both surveyed using nest boxes in the last century.

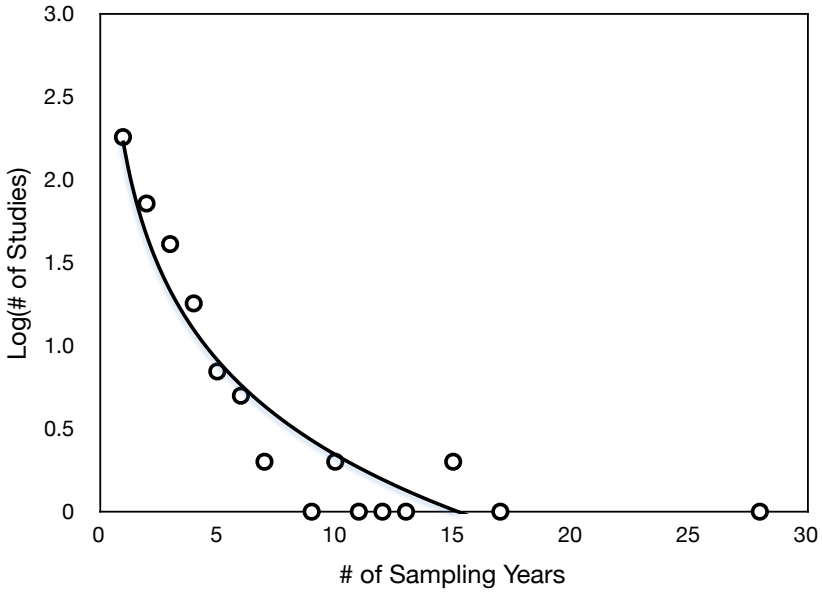


Figure A3. The number of field seasons per study using nest boxes.

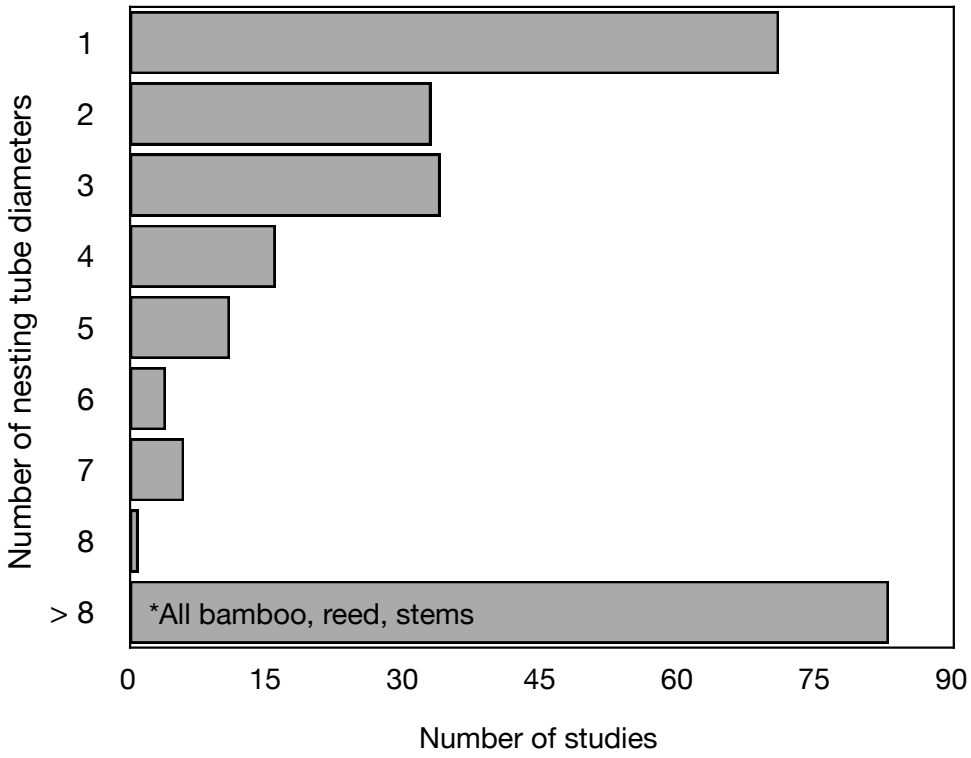


Figure A4. The number of nesting tube diameters per study where they are identified explicitly. Bamboo or reed nesting tubes have natural variation in diameter, and so were listed as having >8 nesting tube diameters (usually identified as being between 2-10mm or 2-20mm in range).

Appendix C. A list of studies used to review literature on cavity-nesting bees and wasps surveyed using nest boxes.

		Nestbox Material							Motivations	
Reference	Location	# year	wood	paper	reed	other	Taxa	Habitat type	1	2
Abel and Wilson (1998) J Kan Entomol Soc	Iowa	1	-	X	-	-	Bee	Cage	Foraging	-
Aguiar and Garófalo (2004) Rev Bras Zool	Brazil	3	-	-	X	-	Both	Forest	Nesting	Behaviour
Aguiar et al. (2005) Rev Braz Biol	Brazil	3	-	X	X	-	Bee	Forest	Diversity	Phenology
Albrecht et al. (2007) J Animal Ecol	Switzerland	2	-	-	X	-	Both	Open	Diversity	Multitrophic
Alonso et al. (2012) Apidologie	Brazil	1	X	-	-	-	Bee	Campus	Design	Nesting
Alston et al. (2007) Environ Entomol	Utah	1	-	X	-	-	Bee	Orchard	Chemistry	Insecticide
Alves-dos-Santos (2003) J Kan Entomol Soc	Brazil	3	X	X	-	-	Both	Campus	Diversity	-
Armbrust (2004) J Kan Entomol Soc	Arizona	1	X	X	-	-	Bee	Open	Nesting	-
Artz et al, (2013) J Insect Conserv	California	1	-	X	-	-	Bee	Orchard	Nesting	Development
Artz et al. (2014) J Econ Entomol	California	1	-	X	-	-	Bee	Orchard	Design	Enhancement
Baker et al (1985) J Kan Entomol Soc	North Carolina	2	-	-	-	-	Bee	-	Nesting	Development
Banos-Picon et al. (2013) Basic Appl Ecol	Spain	1	-	-	X	-	Bee	Agriculture	Enhancement	-
Barthell et al (1998) Environ Entomol	California	2	X	X	-	-	Bee	Agroecosystem	Landscape	Development
Beyer (1987) Ent Soc Wash	Tennessee	1	X	-	-	-	Both	Forest	Diversity	Local
Biddinger et al. (2013) Apidologie	Pennsylvania	1	X	X	-	-	Bee	Orchard	Enhancement	Foraging
Biddinger et al. (2013)	Pennsylvania	1	-	-	X	-	Bee	Open	Chemistry	Insecticide

PLoS One										
Boesi et al. (2005) Florida Entomol	Nepal	2	X	-	-	-	Wasp	Open	Nesting	
Bohart (1955) Proc Entomol Soc Wash	Washington	1	X	-	-	-	Bee	Open	Nesting	Competition
Boone et al. (2004) Can Ent	Ontario	1	-	X	-	-	Both	Forest	Design	Landscape
Bosch (2008) Animal Behav	Spain	3	X	X	-	-	Bee	Orchard	Nesting	Development
Bosch and Kemp (2005) J Econ Entomol	Oregon	1	X	X	-	-	Bee	Agriculture	Population	-
Bosch and Vicens (2002) Ecol Entomol	Spain	1	X	X	-	-	Bee	-	Nesting	Development
Bosch and Vicens (2006) Behav Ecol Sociobio	Spain	1	X	X	-	-	Bee	Agriculture	Nesting	Development
Bosch et al. (2001) Ann Entomol Soc Am	Spain	1	X	-	-	-	Bee	Various	-	Genetics
Bosch et al. (2006) J Econ Entomol	Utah	5	X	X	-	-	Bee	Orchard	Pollination	Enhancement
Budriene (2003) Acta Zool Lith	Lithuania	12	-	-	X	-	Wasp	-	Foraging	Prey
Budriene et al. (2004) Latvijas Entomologs	Lithuania	13	-	-	X	-	Both	Agroecosystem	Nesting	Competition
Budrys et al. (2007) ALARM	Various	1	-	-	X	-	Both	Various	Landscape	-
Bull and Schwarz (1996) Behav Ecol Socio	Australia	1	-	-	X	-	Bee	Campus	Landscape	Nesting
Burkle and Irwin (2009) Environ Entomol	Colorado	1	X	X	-	-	Bee	Open	Foraging	Development
Buschini (2006) Apidologie	Brazil	2	X	-	-	-	Both	Forest	Diversity	-
Buschini and Bergamaschi (2014) Braz J Biol	Brazil	5	X	-	-	-	Wasp	Forest	Development	Sex ratio
Buschini and Fajardo (2010) Acta Zool	Brazil	4	X	-	-	-	Wasp	Various	Nesting	-
Buschini and Wolff (2006) Braz J Biol	Brazil	3	X	-	-	-	Wasp	Forest	Nesting	-
Buschini et al. (2006)	Brazil	3	X	-	-	-	Wasp	Forest	Nesting	-

Braz J Biol										
Buschini et al. (2010) Bras J Biol	Brazil	3	X	-	-	-	Wasp	Various	Foraging	-
Byers (1972) J Kan Entomol Soc	Kansas	1	-	-	X	-	Bee	Urban	Nesting	Competition
Camillo (2004) Rev Biol Trop	Brazil	2	-	X	X	-	Bee	Agroecosystem	Nesting	-
Cane et al. (2011) Apidologie	Utah	1	X	-	-	-	Bee	Agriculture	Foraging	Development
Cardoso and Silveira (2012) Apidologie	Brazil	1	-	-	X	-	Bee	Forest	Nesting	-
Chapman and Stewart (1996) Heredity	Ontario	1	X	-	-	-	Wasp	Agroecosystem	Nesting	Development
Cooper (1957) J Exp Zool	New York	-	X	-	-	-	Wasp	-	Nesting	-
Coudrain et al. (2013) PLoS One	Switzerland	3	-	-	X	-	Wasp	Agriculture	Landscape	-
Coudrain et al. (2014) Front Environ Sci	Switzerland	3	-	-	X	-	Both	Agroecosystem	Landscape	Diversity
Coville (1979) J Kan Entomol Soc	Arizona	1	X	-	-	-	Wasp	Open	Nesting	-
Coville and Griswold (1983) J Kan Entomol Soc	Costa Rica	2	X	-	-	-	Wasp	Forest	Nesting	-
Coville and Griswold (1984) J Kan Entomol Soc	Costa Rica	2	X	-	-	-	Wasp	Various	Nesting	Competition
Cowan (1981) Behav Ecol Sociobiol	Michigan	2	X	-	-	-	Wasp	Agriculture	Development	Foraging
Cowan (1986) Great Lakes Ent	Michigan	1	X	-	-	-	Wasp	-	Parasite	-
Cripps and Rust (1989). Environ Entomol	Utah	-	X	X	-	-	Bee	Open	Foraging	Pollination
Cusumano et al. (2012) Zookeys	Italy	1	-	-	X	-	Wasp	Agriculture	Parasite	-
Daly and Coville (1982) Proc Hawaiian Entomol Soc	Hawaii	2	X	-	-	-	Bee	Urban	Nesting	-
Danks (1971) J Animal Ecol	England	1	-	-	X	-	Bee	-	Nesting	Population

Danks (1971) Trans R Entomol Soc Lond	England	2	-	-	X	-	Both	Urban	Nesting	-
De Lyra Neves et al. (2014) Grana	Brazil	1	-	X	-	Poly	Bee	Various	Foraging	Pollen
Delphia and O'Neill (2012) J Kan Entomol Soc	Montana	1	X	-	-	Poly	Both	Agriculture	Nesting	Competition
Diekotter et al. (2014) Bioenergy	Germany	1	-	-	X	-	Both	Open	Diversity	-
Dobson et al. (2012) Apidologie	Austria	2	X	-	-	-	Bee	Botanical Garden	Foraging	Pollination
Dorado et al. (2011) Ecology	Argentina	2	X	-	-	-	Bee	Open	Diversity	Pollination
Ebeling et al. (2012) Oecologia	Germany	2	-	-	X	-	Both	Open	Diversity	Pollination
Eckhardt et al. (2014) J Animal Ecol	Germany	1	-	-	X	-	Bee	Cage	Foraging	Pollen
Eickwort (1967) J Kan Entomol Soc	Costa Rica	1	-	-	X	-	Bee	Campus	Nesting	
Eltz et al. (2014) Front Ecol Evol	Germany	1	-	-	X	-	Bee	Cage	Nesting	Chemistry
Ercit (2014) Ecol Entomol	Ontario	3	X	-	-	-	Wasp	Various	Foraging	Prey
Ercit and Gwynne (2014) Evolution	Ontario	1	X	-	-	-	Wasp	Open	Development	Reproduction
Ercit et al. (2014) PLoS One	Ontario	3	X	-	-	-	Wasp	Forest	Foraging	-
Evans (1973) Great Basin Nat	Wyoming	6	X	-	-	-	Wasp	Forest	Diversity	-
Evans (1981) Psyche	Australia	2	-	-	-	-	Wasp	Open	Nesting	-
Evans and Matthews (1973) Trans R Entomol Soc Lond	Australia	1	-	-	-	-	Wasp	Open	Nesting	-
Everaars et al. (2011) Land Urb Plann	Germany	1	-	-	X	-	Bee	Urban	Local	-
Fabian et al. (2013) J Animal Ecol	Switzerland	1	-	-	X	-	Both	Various	Landscape	Diversity
Fabian et al. (2014) Ecosphere	Switzerland	1	-	-	X	-	Both	Various	Landscape	Diversity
Fauria and Campan (1998)	Utah	3	-	X	-	Poly	Bee	Various	Nesting	Design

J Insect Behav										
Fauria et al. (2004) Animal Behav	Utah	4	-	-	-	Poly	Bee	Various	Nesting	Design
Fernandez-Triana et al. (2005) Bol Soc Entomol Arag	Cuba	2	-	-	X	-	Wasp	Urban	Nesting	Competition
Filella et al. (2011) Environ Entomol	Spain	1	X	X	-	-	Bee	-	Chemistry	Parasite
Fliszkiewicz et al. (2011) J Apicult Sci	Poland	1	-	-	X	-	Bee	Campus	Development	Overwinter
Fliszkiewicz et al. (2012) Environ Entomol	Poland	1	-	-	X	-	Bee	Campus	Development	Overwinter
Forrest and Thomson (2011) Ecol Mono	Colorado	2	X	X	-	-	Both	Open	Development	Emergence
Frankie et al. (1988) Biotropica	Costa Rica	2	X	-	-	-	Bee	Forest	Nesting	-
Frankie et al. (1993) Biotropica	Costa Rica	5	X	-	-	-	Bee	Forest	Nesting	-
Frankie et al. (1998) Environ Entomol	California	4	X	-	-	-	Both	Forest	Diversity	-
Frankie et al. (2005) J Kan Entomol Soc	Costa Rica	4	X	-	-	-	Bee	Open	Nesting	-
Free and Williams (1970) J Appl Ecol	England	4	-	X	-	-	Bee	-	Nesting	-
Freeman and Jayasingh (1975) Oikos	Jamaica	1	X	-	X	-	Wasp	-	Nesting	Population
Fricke (1991) Great Lakes Ent	Michigan	3	X	-	-	-	Wasp	Open	Nesting	-
Fricke (1992) Great Lakes Ent	Michigan	4	X	-	-	-	Wasp	Campus	Nesting	-
Fricke (1992b) Great Lakes Ent	Michigan	4	X	-	-	-	Wasp	Campus	Nesting	Development
Fricke (1993) Great Lakes Ent	Michigan	1	X	-	-	-	Wasp	Campus	Foraging	-
Frohlich (1983) J Kan Entomol Soc	Utah	1	-	-	X	-	Bee	Cage	Nesting	-
Frohlich and Parker (1983) Psyche	Utah	1	-	-	X	Glass	Bee	Greenhouse	Nesting	Behaviour

Frohlich and Parker (1985) Ann Entomol Soc Am	Utah	-	-	-	-	-	Bee	-	Nesting	Development
Frohlich and Tepedino (1986) Evolution	Utah	1	-	X	X	-	Bee	Open	Nesting	Sex ratio
Fruend et al. (2013) Ecology	Germany	1	-	-	X	-	Bee	Cage	Diversity	Pollination
Fruend et al. (2013) Oecologia	Germany	1	-	-	X	-	Bee	Orchard	Development	Overwinter
Fye (1965) Can Ent	Ontario	3	-	-	X	-	Wasp	Open	Nesting	Diversity
Gardner and Spivak (2014) Ann Entomol Soc Am	Minnesota	3	-	-	X	-	Bee	Forest	Nesting	Diversity
Garofelo (1998) Rev Bras Zool	Brazil	1	X	-	X	-	Both	Forest	Nesting	-
Gaston et al. (2005) Biol Conserv	England	3	X	X	-	-	Bee	Urban	Diversity	-
Gathmann and Tscharntke (2002) J Animal Ecol	Germany	2	-	-	X	-	Both	Agroecosystem	Diversity	Foraging
Gazola and Garofalo (2003) J Kan Entomol Soc	Brazil	4	-	X	-	-	Bee	Campus	Parasite	-
Gazola and Garogalo (2009) Genet Mol Res	Brazil	3	-	-	X	-	Both	Forest	Population	Diversity
Gerber and Klostermeyer (1970) Science	Washington	1	-	-	-	Plastic	Bee	Cage	Nesting	Sex ratio
Giejdasz and Wilkaniec (2002) J Apicult Sci	Poland	2	-	-	X	-	Bee	-	Development	
Goerzen et al. (1995) J Appl Entomol	Saskatchewan	3	X	X	-	-	Bee	Agriculture	Design	Dispersal
Goettel et al. (1997) Can Ent	Saskatchewan	11	-	-	-	Poly	Bee	Agriculture	Parasite	-
Gruber et al. (2011) Apidologie	Germany	3	-	-	X	-	Bee	Various	Enhancement	-
Guedot et al (2007) J Kan Entomol Soc	Utah	3	X	X	-	-	Bee	Orchard	Enhancement	Design
Guedot et al. (2005) J Apicult Res	Utah	2	X	-	-	-	Bee	Agriculture	Design	Nesting
Guedot et al. (2006) J Econ Entomol	Utah	1	X	-	-	Poly	Bee	Agriculture	Design	-

Guedot et al. (2009) Ecol Entomol	Utah	1	X	X	-	-	Bee	Orchard	Foraging	-
Guisse and Miller (2011) Pan Pac Entomol	California	1	X	X	-	-	Bee	Open	Landscape	-
Haider et al. (2013) Func Ecol	Various Europe	1	-	-	X	-	Bee	Cage	Development	Pollen
Hallett (2001) Am Bee J	Ontario	7	X	-	-	-	Bee	Open	Diversity	-
Harris (1994) New Zeal Entomol	New Zealand	1	X	-	-	-	Wasp	Various	Nesting	-
Harris (1994) New Zealand J Crop Hort	New Zealand	1	X	-	-	-	Wasp	Urban	Foraging	Prey
Hartman (1944) Psyche	Conneticut	1	-	-	-	Glass	Bee	-	Nesting	-
Hawkins (1975) J Kan Entomol Soc	Tennessee	2	X	-	-	-	Bee	Open	Nesting	-
Hobbs (1968) Can Ent	Alberta	2	X	X	-	-	Bee	Lab	Design	Parasite
Hobbs and Richards (1976) Can Ent	Alberta	4	X	-	-	-	Bee	Agriculture	Nesting	Development
Hodgson et al. (2011) J Insect Sci	Utah	1	X	X	-	-	Bee	Agriculture	Development	Physiology
Holzschuh et al. (2009) Ecol Appl	Germany	1	-	-	X	-	Both	Forest	Diversity	Parasitism
Holzschuh et al. (2010) J Animal Ecol	Germany	2	-	-	X	-	Both	Agriculture	Landscape	Diversity
Holzschuh et al. (2013) Oecologia	Germany	1	-	-	X	-	Bee	Agriculture	Local	Nesting
Horne (1995) Ann Entomol Soc Am	Alberta	2	-	-	-	-	Bee	Open	Nesting	Pollination
Hranitz et al. (2009) Environ Entomol	California	2	X	X	-	-	Bee	Open	Local	Nesting
Hudewenz and Klein (2013) J Insect Conserv	Germany	1	-	-	X	-	Bee	Open	Nesting	Population
Hurst (1997) Aus J Ecol	Australia	1	-	-	X	-	Bee	Campus	Nesting	Behaviour
Inoka et al. (2006) Biodiv	Sri Lanka	?	X	-	X	-	Bee	Agroecosystem	Diversity	-
Itino (1992) Res Popul Ecol	Japan	2	-	-	X	-	Wasp	Forest	Foraging	Competition

Ivanov (2006) Ent Rev	Crimea	8	-	-	X	-	Bee	Open	Nesting	-
Ivanov et al. (2013) Ent Rev	Crimea	-	-	-	X	-	Bee	Open	Nesting	-
James (2005) J Econ Entomol	Utah	1	X	-	-	-	Bee	Lab	Design	Parasite
Jauker et al. (2012) Basic Appl Ecol	Germany	2	-	-	X	-	Bee	Various	Enhancement	Pollination
Jayasingh and Freeman (1980) Biotrop	Jamaica	3	X	-	X	-	Both	Various	Population	-
Jayasingh and Taffe (1982) Ecol Entomol	Jamaica	2	-	-	X	-	Wasp	Open	Nesting	-
Jaycox (1967) J Kan Entomol Soc	New York	2	X	-	-	-	Bee	Open	Nesting	-
Jenkins and Matthews (2004) J Kan Entomol Soc	Georgia/ Carolina	1	X	-	-	-	Both	Forest	Diversity	Nesting
Jennings and Parker (1987) Great Lakes Ent	Maine	6	X	-	-	-	Wasp	Forest	Nesting	Forgaing
Johnson (1980) J Kan Entomol Soc	Indiana	2	X	-	-	-	Bee	-	Development	Cocoon
Jun and Hui-Zhen (1995) Entomol Knowl	China	-	-	-	X	-	Bee	Agriculture	Enhancement	Nesting
Junquiera and Augusto (2012) Ann Entomol Soc Am	Brazil	2	-	-	X	-	Bee	Orchard	Enhancement	-
Kamke et al. (2008) J Kan Entomol Soc	Brazil	4	X	-	X	-	Bee	Forest	Nesting	Parasite
Kemp and Bosch (2001) Ann Entomol Soc Am	Utah	1	-	-	-	Poly	Bee	Agriculture	Development	Overwinter
Kessler et al. (2009) Ecol Appl	Indonesia	1	-	-	X	-	Both	Forest	Diversity	Landscape
Kim (1992) Ann Entomol Soc Am	California	-	-	-	-	-	Bee	-	Design	-
Kim (1997) Ecol Entomol	California	1	X	-	-	-	Bee	Open	Nesting	Population
Kim and Thorp (2001) Oecologia	California	1	X	X	-	-	Bee	Agriculture	Nesting	Development
Klein et al. (2000) Conserv Biol	Sulawesi	2	-	-	X	-	Both	Agroecosystem	Diversity	Parasite

Klein et al. (2004) J Animal Ecol	Indonesia	1	-	-	X	-	Both	Agroecosystem	Foraging	Population
Klein et al. (2006) J Animal Ecol	Indonesia	1	-	-	X	-	Both	Agroecosystem	Landscape	Diversity
Klostermeyer and Gerber (1969) Ann Entomol Soc Am	Washington	1	X	X	-	-	Bee	Agriculture	Nesting	Behaviour
Klostermeyer et al. (1973) J Kan Entomol Soc	Washington	2	-	-	-	-	Bee	Greenhouse	Foraging	Sex ratio
Koerber and Medler (1958) Trans Am Entomol Soc	Wisconsin	1	-	-	X	-	Both	Agriculture	Diversity	Landscape
Kraemer and Favi (2005) Environ Entomol	Vermont	5	X	-	-	-	Bee	Orchard	Parasite	Pollination
Kraemer et al. (2014) Environ Entomol	Virginia, Carolina	3	X	-		-	Bee	Orchard	Nesting	Pollination
Krewenka et al. (2011) Biol Conserv	Germany	1	-	-	X	-	Both	Open	Landscape	Diversity
Krombein (1958) Trans Am Entomol Soc	North Carolina	9	X	-	-	-	Wasp	Various	Nesting	Parasite
Kruess and Tscharntke (2002) Conserv Biol	Germany	1	-	-	X	-	Both	Open	Diversity	Parasite
Krunic (1972) Can Ent	Alberta	1	-	-	-	-	Bee	Agriculture	Nesting	Development
Krunic and Stanisavljevic (2006) Eur J Entomol	Serbia	6	X	X	X	-	Bee	Orchard	Enhancement	-
Kuhn and Ambrose (1984) J Kan Entomol Soc	Virginia	2	X	-	-	-	Bee	Orchard	Enhancement	Foraging
Laliberte and Tylianakis (2010) Ecology	Ecuador	1	-	-	X	-	Both	Agroecosystem	Landscape	Parasite
Levin (1957) J Econ Entomol	Utah	-	X	-	-	-	Bee	-	Design	-
Levin (1966) J Kan Entomol Soc	Utah	4	X	-	-	-	Bee	Open	Nesting	-
Levin and Haydak (1957) Bee World	Utah	1	-	-	-	Plastic	Bee	Open	Foraging	Pollen
Longair (1981) Evolution	Ontario	1	X	-	-	-	Wasp	Open	Development	Sex ratio
Loyola and Martins (2006) Neotrop Entomol	Brazil	1	X	-	-	-	Both	Forest	Nesting	Mortality
Loyola and Martins (2008)	Brazil	1	X	-	-	-	Both	Forest	Landscape	Diversity

Basic Appl Ecol										
Loyola and Martins (2011) Rev Bras Entomol	Brazil	1	X	-	-	-	Both	Various	Landscape	Diversity
MacIvor (2015) TIEE	Ontario	3	-	X	-	-	Both	Urban	Diversity	-
MacIvor and Moore (2013) Ecosphere	Ontario	1	-	X	-	-	Bee	Urban	Nesting	-
MacIvor and Packer (2015) PLoS One	Ontario	3	-	X	-	-	Both	Urban	Diversity	-
MacIvor and Salehi (2014) Environ Ent	Ontario	2	-	X	-	-	Bee	Urban	Parasite	-
MacIvor et al. (2014) Urb Ecosyst	Ontario	1	-	X	-	-	Bee	Urban	Pollination	Pollen
Maeta and Sugiura (1990) Jpn J Ent	Japan	1	-	X	X	-	Bee	Cage	Development	Size
Magalhães and Freitas (2013) Apidologie	Brazil	1	X	-	-	-	Bee	Agriculture	Landscape	Design
Martins et al. (2012) Neotrop Entomol	Brazil	2	X	X	-	-	Both	Agriculture	Design	-
Mathews and Mathews (1968) Psyche	Arizona	1	X	-	-	-	Wasp	Open	Nesting	Foraging
Matos et al. (2012) Biotrop	Brazil	1	-	-	X	-	Both	Agriculture	Diversity	-
Matsumoto and Makino (2011) Entomol Sci	Japan	1	-	-	X	-	Both	Forest	Diversity	Design
Matthews (2000) J Hym Res	Arizona	1	-	-	X	-	Wasp	-	Nesting	-
Mayer (1994) J Ent Soc Brit Columbia	Washington	3	X	-	-	-	Bee	Agriculture	Nesting	Sex ratio
Medler (1959) Can Ent	Wisconsin	1	-	-	X	-	Bee	Agriculture	Nesting	-
Medler (1965) J Kan Entomol Soc	Wisconsin	10	-	-	X	-	Wasp	-	Nesting	-
Medler (1967) Am Mid Nat	Wisconsin	10	-	-	X	-	Wasp	Various	Nesting	-
Medler and Fye (1956) Ann Entomol Soc Am	Wisconsin	-	-	-	X	-	Wasp	Various	Nesting	-
Medler and Koerber (1957) Ann Entomol Soc Am	Wisconsin	-	-	-	X	-	Wasp	Various	Nesting	-

Mesquita and Augusto (2011) Trop Zool	Brazil	-	-	-	-	-	Bee	Open	Diversity	Parasite
Moron et al. (2008) Wetlands	Poland	1		X	X	-	Bee	Open	Diversity	-
Moron et al. (2012) J Appl Ecol	England	3	-	-	X	-	Bee	Open	Diversity	Land
Moron et al. (2013) J Insect Conserv	England	3	-	-	X	-	Bee	Open	Development	Sex ratio
Morris et al. (2014) Ecography	Australia	1	-	-	X	-	Both	Forest	Foraging	Diversity
Munstern-Swendsen and Calabuig (2000) Ecol Entomol	Denmark	1	-	-	X	-	Bee	Open	Parasite	-
Musicante and Salvo (2010) Rev Biol Trop	Argentina	1	-	-	X	-	Wasp	Forest	Nesting	-
Nascimento and Garofalo (2014) Sociobiol	Brazil	2	-	X	X	-	Wasp	Forest	Development	Sex ratio
O'Neill and O'Neill (2003) J Kan Entomol Soc	Montana	2	-	X	-	Poly	Wasp	Open	Nesting	Foraging
O'Neill and O'Neill (2009) Entomol Amer	New York	2	X	X	-	-	Wasp	Forest	Nesting	-
O'Neill and O'Neill (2010) Northeast Nat	New York	4	X	X	-	-	Both	Forest	Diversity	-
O'Neill et al (2014) PeerJ	Montana	1	X	-	-	-	Bee	Agriculture	Development	Body Size
O'Neill et al. (2010) Ann Soc Entomol Am	Montana	1	-	X	-	-	Bee	Agriculture	Nesting	Population
O'Neill et al. (2011) Environ Entomol	Montana, Indiana	3	-	-	-	Poly	Bee	Agriculture	Development	Overwinter
O'Neill and O'Neill (2013) Entomol Soc Wash	Washington	-	-	-	-	-	Both	Forest	Diversity	-
Oku and Nishida (1999) Ann Entomol Soc Am	Japan	1	-	-	X	-	Wasp	Open	Nesting	Competition
Oku and Nishida (1999) Res Popul Ecol	Japan	5	-	-	X	-	Wasp	Forest	Development	Sex ratio
Oliveira and Schlindwein (2009) J Econ Entomol	Brazil	3	X	X	-	-	Bee	Orchard	Enhancement	Pollination
Paini (2004)	Australia	2	X	-	-	-	Bee	Forest	Nesting	Biology

Aus J Entomol										
Paini and Bailey (2002) Ecol Entomol	Australia	2	X	-	-	-	Bee	Open	Population	Sex ratio
Park et al. (2008) J Appl Entomol	West Virginia	1	-	X	-	-	Bee	Lab	Parasite	-
Parker (1978) J Kan Entomol Soc	California	15	-	-	X	-	Bee	Open	Nesting	Biology
Parker (1981) Southwest Entomol	Arizona	15	-	-	X		Bee	Open	Nesting	Biology
Parker (1984a) J Kan Entomol Soc	Utah	1	-	X	-	-	Bee	Various	Nesting	Biology
Parker (1984b) J Kan Entomol Soc	California/ Arizona	4	-	-	X	-	Wasp	Various	Nesting	Parasite
Parker (1986) J Kan Entomol Soc	Utah	1		X	X	-	Bee	Open	Nesting	Biology
Parker and Frohlich (1983) Environ Entomol	Utah	1	-	-	X	-	Bee	Agriculture	Foraging	Enhancement
Parker and Pedersen (1975) Environ Entomol	Utah	1	-	-	X	-	Bee	Agriculture	Foraging	Development
Parker and Tepedino (1982) J Kan Entomol Soc	Utah	1	-	-	X	-	Bee	Open	Nesting	-
Payne et al. (2011) Apidologie	New York	1	-	-	X	-	Bee	Cage	Nesting	Landscape
Pechuman (1967) J NY Entomol Soc	New York	1	X	-	-	-	Bee	-	Nesting	Behaviour
Pereira-Peixoto et al. (2014) J Insect Conserv	Germany	1	-	-	-	Plastic	Both	Urban	Local	Diversity
Peruquetti (2005) J Kan Entomol Soc	Brazil	2	-	-	X	-	Wasp	Forest	Nesting	-
Peterson and Roitberg (2006) Behav Ecol Sociobiol	Alberta	1	X	-	-	-	Bee	Agriculture	Foraging	Sex ratio
Philips and Klostermeyer (1978) J Kan Entomol Soc	Washington	2	-	-	-	-	Bee	Cage	Nesting	Behaviour
Pina and Aguiar (2011) Sociobiol	Brazil	1	X	X	-	-	Bee	Orchard	Diversity	-

Pitts-Singer and James (2008) J Econ Entomol	Various	3	X	-	-	-	Bee	Agriculture	Nesting	Landscape
Polidori et al. (2013) Comptes Rendus Biologies	Italy	1	X	-	-	-	Wasp	Various	Local	Design
Praz et al. (2008) Apidologie	Switzerland	1	-	-	X	-	Bee	Cage	Foraging	Pollen
Praz et al. (2008) Ecology	Switzerland	1	-	-	X	-	Bee	Cage	Foraging	Development
Quiroz-Garcia et al. (2001) J Kan Entomol Soc	Mexico	3	X	-	-	-	Bee	Forest	Nesting	Foraging
Radmacher and Strohm (2010) Apidologie	Germany	1	-	-	-	Poly	Bee	Campus	Local	Development
Radmacher and Strohm (2011) Apidologie	Germany	1	-	-	-	Poly	Bee	Botanical Garden	Local	Development
Rank et al. (1990) J Appl Entomol	Oregon	2	X	X	-	-	Bee	Open	Parasite	-
Raw (1972) Trans R Ent Soc London	England	2	-	X	-	-	Bee	Open	Nesting	-
Raw (1974) Oikos	England	2	-	X	-	-	Bee	Open	Pollination	Pollen
Raw (1976) Behav	England	2	-	-	X	-	Bee	Urban	Nesting	Behaviour
Rosen and Hall (2012) Am Mus Nov	Florida	1	X	-	-	-	Bee	Marsh	Nesting	Development
Rossi et al. (2010) Animal Behav	Utah	2	-	X		Poly	Bee	Agriculture	Nesting	-
Rothschild (1979) J Kan Entomol Soc	Alberta	-	-	-	-	Poly	Bee	-	Population	Local
Roubik and Villanueva-Gutierrez (2009) Biol J Linn Soc	Mexico	17	X	-	-	-	Bee	Forest	Foraging	Pollen
Rubene et al. (2014) Insect Conserv Div	Sweden	1	-	-	X	-	Both	Forest	Sampling	Diversity
Rust (1986) J Kan Entomol Soc	Nevada	2	X	-	-	-	Bee	Urban	Nesting	-
Rust (1990) Environ Entomol	Utah	-	X	X	-	-	Bee	Open	Landscape	Foraging
Rust (1993) Ann Entomol Soc Am	Utah	-	X	X	-	-	Bee	Open	Nesting	Foraging
Rust et al. (1974)	Utah	1	X	X	-	-	Bee	Greenhouse	Nesting	-

J Nat Hist										
Sabino and Antonini (2011) J Kan Entomol Soc	Brazil	4	-	X	-	-	Bee	Forest	Nesting	-
Sagiura and Maeta (1989) Entomol Soc Jpn	Japan	1	-	X	X	-	Bee	Cage	Development	Sex ratio
Sampson et al. (2004) Small Fruits Review	Missouri	1	-	-	X	-	Bee	Agriculture	Pollination	Enhancement
Sandrock et al. (2013) Agric Forest Entomol	Switzerland	1	X	-	-	-	Bee	Agriculture	Chemistry	Insecticide
Santoni and Del Lama (2006) Rev Bras Entomol	Brazil	4	-	-	X	-	Wasp	-	Nesting	-
Santoni and Lama (2007) Rev Bras Entomol	Brazil	3	-	-	X	-	Wasp	Urban	Nesting	-
Santos (2003) J Kan Entomol Soc	Brazil	3	X	-	-	-	Both	-	Nesting	Diversity
Scaramozzino et al. (1991) Ethol Ecol Evol	Italy	2	-	-	X	-	Wasp	Forest	Nesting	Behaviour
Schuepp et al. (2011) Oecologia	Switzerland	1	-	-	X	-	Bee	Urban	Landscape	Diversity
Schulze et al. (2012) Flora	Switzerland	1	X	-	-	-	Bee	Cage	Pollination	Foraging
Scott (1994) Great Lake Entomol	Michigan	2	X	-	-	-	Bee	Open	Nesting	Phenology
Scott (1996) J Kan Entomol Soc	Michigan	1	X	-	-	-	Bee	Open	Pollination	Pollen
Scott and Strickler (1992) J Kan Entomol Soc	Michigan	3	X	-	-	-	Bee	Forest	Parasite	-
Sears et al. (2001) Am Mid Nat	California	2	X	-	-	-	Wasp	Marsh	Nesting	Behaviour
Sedivy et al. (2011) Func Ecol	Switzerland	1	-	-	X	-	Bee	Agriculture	Development	Pollen
Seidelmann (1999) Apidologie	Germany	2	X	-	-	-	Bee	Botanical Garden	Nesting	Parasite
Seidelmann et al. (2010) Behav Ecol Sociobiol	Germany	1	X	-	X	-	Bee	Botanical Garden	Development	Sex ratio
Seidelmann et al. (2014) Ecol Entomol	Germany	1	X	-	-	-	Bee	Botanical Garden	Development	Body size

Sekita and Yamada (1993) JARQ	Japan	1	-	-	X	Plastic	Bee	Orchard	Chemistry	Insecticide
Sgolastra et al. (2011) J Insect Physio	Utah	1	X	X	-	-	Bee	Orchard	Development	Metabolism
Sgolastra et al. (2012) J Insect Physio	Spain	1	-	X	-	-	Bee	Various	Development	Emergence
Sheffield et al. (2008) Can Ent	Nova Scotia	2	-	X	-	-	Bee	Agriculture	Diversity	-
Sheffield et al. (2008) J Entomol Soc Ont	Nova Scotia	1	X	-	-	-	Bee	Agriculture	Development	Overwinter
Sheffield et al. (2014) J Poll Ecol	Nova Scotia	2	X	-	-	-	Bee	Orchard	Pollination	Enhancement
Sihag, R. C. (1993) J Apicult Res	India	1	-	-	X	-	Bee	Agriculture	Foraging	Nesting
Silva et al. (2014) Neotrop Entomol	Brazil	2	-	-	-	Plastic	Bee	Forest	Landscape	Development
Sobek et al. (2009) Forest Ecol Manage	Germany	1	-	-	X	-	Both	Forest	Landscape	Diversity
Stangler et al. (2014) Biodivers Conserv	Costa Rica	1	-	-	X	-	Both	Forest	Landscape	Diversity
Stanley and Stout (2013) J Appl Ecol	Ireland	2	-	-	X	-	Bee	Agriculture	Foraging	Diversity
Steckel et al. (2014) Biol Conserv	Germany	1	-	-	X	-	Both	Open	Landscape	Diversity
Steffan-Dewenter and Schiele (2004) Entomol Gener	Germany	4	-	-	X	-	Bee	Orchard	Development	Nesting
Steffan-Dewenter and Schiele (2008) Ecology	Germany	5	-	-	X	-	Bee	Orchard	Nesting	Population
Steffan-Dewenter and Tscharntke (2000) Oecologia	Germany	1	-	-	X	-	Bee	Agriculture	Foraging	Competition
Steffan-Dewenter et al. (2002) Ecol Entomol	Germany	1	-	-	X	-	Both	Agroecosystem	Landscape	Diversity
Stephen (1961) J Econ Entomol	Oregon	1	X	X	-	-	Bee	-	Enhancement	Design
Stephen and Osgood (1965)	Oregon	4	X	X	X	Poly	Bee	Open	Nesting	Design

J Econ Entomol										
Strickler et al. (1996) J Kan Entomol Soc	Michigan	7	X	-	-	-	Bee	Forest	Diversity	Nesting
Stubbs et al. (1994) J Kan Entmool Soc	Maine	2	-	X	-	-	Bee	Agriculture	Enhancement	-
Stubbs et al. (1997) Northeastern Nat	Maine	3	X	-	-	-	Bee	Agriculture	Enhancement	Pollination
Sugiura (1994) J Ethol	Japan	1	-	-	X	-	Bee	Cage	Population	-
Taki et al. (2004) Can Ent	Ontario	1	-	X	-	-	Both	Forest	Design	-
Taki et al. (2007) J Appl Entomol	Ontario	2	-	X	-	-	Wasp	Forest	Local	Design
Taki et al. (2008) J Insect Conserv	Ontario	1	-	X	-	-	Wasp	Forest	Landscape	Local
Tasei and Picart (1972) Apidologie	France	1	X	-	X	-	Bee	Agriculture	Nesting	Pollen
Taylor (1922) Psyche	Mass., USA	1	-	-	-	Glass	Wasp	-	Nesting	-
Tepedino (1980) J Kan Entomol Soc	Utah	1	-	X	-	-	Bee	Agriculture	Development	Sex ratio
Tepedino (1983) J Apicult Res	Utah	1	X	X	-	-	Bee	Agriculture	Enhancement	Pollen
Tepedino and Frohlich (1982) J NY Ent Soc	Utah	1	-	X	-	-	Bee	Open	Development	Sex ratio
Tepedino and Frohlich (1984) Behav Ecol Sociobiol	Utah	1	X	X	-	-	Bee	Agriculture	Development	
Tepedino and Parker (1983) Southwest Entomol	California	1	-	-	X	-	Bee	Open	Nesting	Develop
Tepedino and Parker (1986) J Econ Entomol	Utah	1	X	X	-	-	Bee	Agriculture	Development	Overwinter
Tepedino and Parker (1986) Pan-Pac Entomol	Utah	1	X	X	-	-	Bee	Agriculture	Development	Cocoon
Tepedino and Parker (1988) Ann Entomol Soc Am	Utah	3	-	X	-	-	Bee	Agriculture	Population	

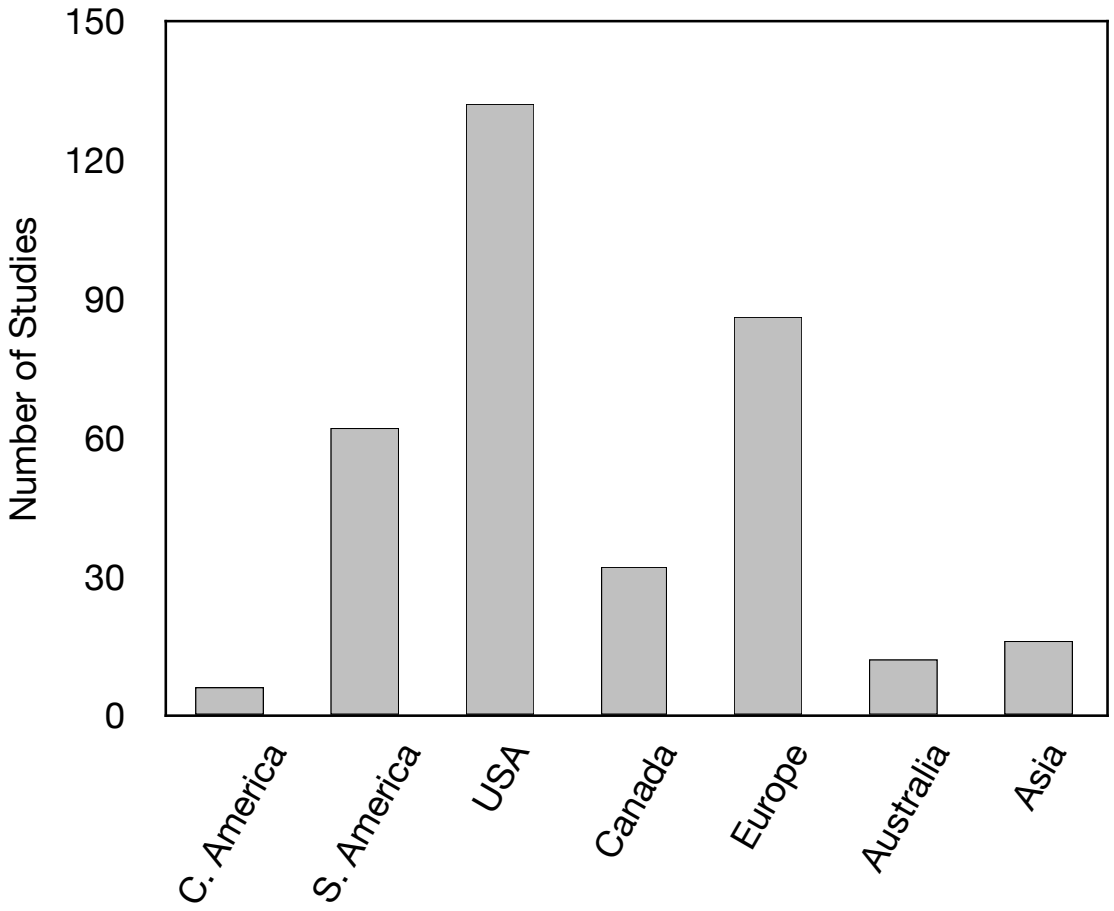
Tepedino and Parker (1988) J Kan Entomol Soc	Wyoming	1	-	-	X	-	Bee	Open	Nesting	Development
Tepedino and Torchio (1982) Oikos	Idaho	6	X	X	-	Poly	Bee	Open	Population	Sex ratio
Tepedino and Torchio (1989) Ann Entomol Soc Am	Utah	1	X	X		-	Bee	Greenhouse	Design	Sex ratio
Tepedino et al. (1979) Pan-Pac Entomol	Wyoming	1	X	-	X	-	Bee	Open	Nesting	Recognition
Tepedino et al. (1984) Apidologie	Utah	1	X	-	-	-	Bee	Greenhouse	Nesting	Development
Teper and Bilinski (2009) J Apicult Sci	Poland	3	-	-	X	-	Bee	Agriculture	Enhancement	Pollination
Teper et al. (2007) J Apicult Sci	Poland	2	-	-	X	-	Bee	Agriculture	Pollination	Pollen
Teper et al. (2008) J Apicult Sci	Poland	2	-	-	X	-	Bee	Agriculture	Pollination	Pollen
Thiele (2002) J Kan Entomol Soc	Costa Rica	2	X	-	-	-	Bee	Forest	Nesting	-
Thiele (2004) Stud Neotrop Fauna Environ	Costa Rica	1	X	-	-	-	Bee	Forest	Nesting	-
Thorp et al. (1992) Calif Agric	California	-	X	-	-	-	Bee	Agriculture	Diversity	Competition
Torchio (1976) J Kan Entomol Soc	Utah	2	-	X	-	-	Bee	Orchard	Enhancement	-
Torchio (1980) J Kan Entomol Soc	Utah	1	-	-	-	-	Bee	-	Development	Cocoon
Torchio (1981) J Kan Entomol Soc	California	1	X	X	-	Poly	Bee	Orchard	Enhancement	Pollination
Torchio (1981b) J Kan Entomol Soc	California	1	X	X	-	Poly	Bee	Orchard	Nesting	-
Torchio (1983) J Kan Entomol Soc	Idaho	1	X	X	-	-	Bee	Agriculture	Chemistry	Insecticide
Torchio (1984a) J Kan Entomol Soc	Utah	1	X	X	-	Poly	Bee	Orchard	Design	Enhancement
Torchio (1984b) J Kan Entomol Soc	Idaho	1	-	X	-	-	Bee	-	Diversity	-

Torchio and Asensio (1985) J Kan Entomol Soc	Utah	2	X	X	-	-	Bee	Orchard	Enhancement	Management
Torchio and Tepedino (1980) Evolution	Utah	1	-	X	-	-	Bee	Open	Nesting	-
Torchio and Tepedino (1982) Psyche	Utah	2	X	X	-	-	Bee	Open	Development	Emergence
Toretta (2014) J Nat Hist	Argentina	1	-	-	X	-	Wasp	Forest	Development	-
Toretta et al. (2012) Apidologie	Argentina	2	-	-	X	-	Bee	Open	Nesting	-
Tormos et al. (2005) Fla Entomol	Spain	3	-	-	X	-	Wasp	-	Nesting	-
Trostle and Torchio (1994) J Kan Entomol Soc	Utah	3	-	-	-	Glass	Bee	Greenhouse	Nesting	Development
Tscharntke et al. (1998) J Appl Ecol	Germany	1	-	-	X	-	Both	Agroecosystem	Landscape	Diversity
Tylianakis et al. (2005) Ecology	Ecuador	1	-	-	X	-	Bee	Forest	Diversity	-
Tylianakis et al. (2006) Ecology	Ecuador	1	-	-	X	-	Both	Agriculture	Diversity	Multitropic
Tylianakis et al. (2006) J Biogeog	Ecuador	1	-	-	X	-	Bee	Forest	Diversity	-
Tylianakis et al. (2007) Nat Lett	Ecuador	1	-	-	X	-	Bee	Forest	Diversity	-
Vanderberg et al. (1980) Appl Environ Microbiol	California	1	-	X	-	-	Bee	Open	Nesting	Ecology
Vandenberg (1995) J Econ Entomol	New York	1	X	X	-	-	Bee	Cage	Nesting	-
Veddeler et al. (2010) Oecologia	Ecuador	1	-	-	X	-	Both	Agroecosystem	Multitrophic	Parasite
Vicens and Bosch (2000) Environ Entomol	Spain	1	X	-	-	-	Bee	Orchard	Enhancement	-
Vickruck and Richards (2012) Animal Behav	Ontario	1	-	-	X	-	Bee	Campus	Nesting	Ecology
Vieira and Garofalo (2000) Apidologie	Brazil	1	-	X	-	-	Bee	Campus	Nesting	Behaviour
Vinson and Frankie (2000) Ann Entomol Soc Am	Costa Rica	3	X	-	-	-	Bee	Forest	Nesting	Behaviour

Vinson et al. (1996) Fla Entomol	Costa Rica	-	X	-	-	-	Bee	Forest	Chemistry	Ecology
Vinson et al. (2010) J Kan Entomol Soc	Costa Rica	5	X	-	-	-	Bee	Forest	Nesting	-
Waller (1969) J Econ Entomol	Utah	1	-	-	-	-	Bee	Agriculture	Chemistry	Insecticide
Wei et al. (2002) Can Ent	China	3	X	X	-	-	Bee	Orchard	Pollination	Enhancement
West and McCutcheon (2009) Int J Fruit Sci	West Virginia	2	-	X	-	-	Bee	Orchard	Pollination	Enhancement
Westphal et al. (2008) Ecol Mono	Various Europe	1	-	X	X	-	Bee	Various	Diversity	Landscape
Whitfield et al. (1987) Can Ent	Alberta	1	X	-	-	-	Bee	Agriculture	Development	-
Wilkaniec and Giejdasz (2003) J Apicult Sci	Poland	1	--	-	X	-	Bee	Agriculture	Pollination	Enhancement
Wilkaniec et al. (2004a) J Apicult Sci	Poland	1	-	-	X	-	Bee	Campus	Development	Foraging
Wilkaniec et al. (2004b) J Apicult Sci	Poland	1	-	-	X	-	Bee	Open	Pollination	-
Williams (2003) Oecologia	Utah	2	X	X	-	-	Bee	Open	Foraging	Pollen
Williams and Kremen (2007) Ecol Appl	California	1	X	-	-	-	Bee	Agroecosystem	Landscape	Enhancement
Williams and Tepedino (2003) Behav Ecol	Utah	2	X	X	-	-	Bee	Open	Foraging	Pollen
Wilson and Holway (2010) Ecology	Hawaii	3	X	-	-	-	Wasp	Forest	Nesting	Competition
Wilson et al. (1999) J Iowa Acad Sci	Iowa	1	-	X	-	Poly	Bee	Urban	Enhancement	Population
Woodward (1996) Aus J Entomol	Australia	1	X	-	-	-	Bee	Open	Diversity	Competition
Wrightman and Rogers (1978) Oecologia	New Zealand	2	X	-	-	-	Bee	Agriculture	Nesting	Development
Yamamoto et al. (2014) Apidologie	Brazil	6	-	-	-	-	Bee	Orchard	Pollination	-
Yocum et al. (2005) J Insect Physio	Utah	1	X	X	-	-	Bee	Lab	Development	Overwinter

Yoshimoto (1969) J Entomol Hawaii Soc	Hawaii	1	-	-	X	-	Bee	Urban	Nesting	-
Zajdel et al. (2014) Ann Warsaw Univ of Life Sci	Poland	1	-	-	X	-	Bee	Various	Nesting	Behaviour
Zanette et al. (2004) Trop Zool	Brazil	2	-	-	X	-	Wasp	Campus	Nesting	Sex ratio
Zillikens and Steiner (2004) J Kan Entomol Soc	Brazil	2	X	-	-	-	Bee	Forest	Nesting	Parasite
Zillikens et al. (2001) Studies Neotrop Fauna Environ	Brazil	1	-	-	X	-	Bee	Forest	Nesting	-
Zurbuchen et al. (2010) Apidologie	Switzerland	?	X	-	X	-	Bee	Agroecosystem	Landscape	Diversity
Zurbuchen et al. (2010) J Animal Ecol	Switzerland	1	X	-	-	-	Bee	Agriculture	Foraging	-

Appendix D. Number of studies carried out summed by geographic locations.



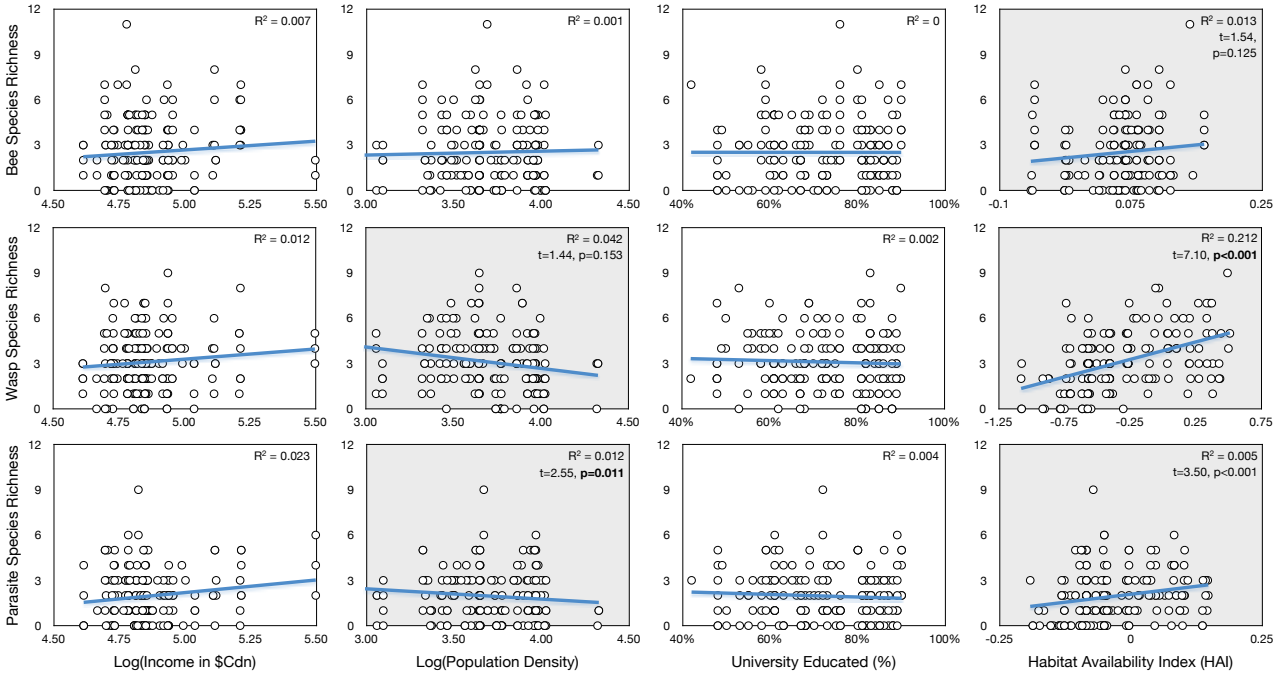
Appendix E. List of all species of bees, wasps, and parasites, and their relative abundance from the total sample and presence in each annual sample. In the Type column, B=Bees, W=Wasps, P=Parasite. A parasite can be a bee or a wasp and are labeled if so. Presence is denoted as either a Y=Yes, or N=No. A bolded species names indicates they are not native to the study region. "*" parasite that emerged from a caterpillar collected by a *Symmorphus* wasp. "+" cryptic fly genus and we await barcode results to determine whether there are more than one species.

Order	Family	Genus	Species	Type	2011	2012	2013	Relative Abund
Hymenoptera	Apidae	*Anthophora*	*terminalis* Cresson	B	N	N	Y	0.004%
	Megachildae	*Megachile*	*brevis* Say	B	N	Y	N	0.081%
			campanulae (Robertson)	B	Y	Y	Y	4.789%
			centuncularis (Linnaeus)	B	Y	Y	Y	3.881%
			frigida Smith	B	N	Y	Y	0.332%
			inermis Provancher	B	Y	N	N	0.093%
			mendica Cresson	B	Y	Y	N	0.063%
			pugnata Say	B	Y	Y	Y	1.363%
			relativa Cresson	B	Y	Y	Y	0.574%
			rotundata Fabricius	B	Y	Y	Y	7.722%
			sculpturalis Smith	B	N	N	Y	0.056%
		Heriades	*carinata* Cresson	B	Y	Y	Y	3.052%
			variolosa (Cresson)	B	Y	N	N	0.015%
		Chelostoma	***campanularum*** (Kirby)	B	N	Y	Y	0.107%
			rapunculi (Lepeletier)	B	Y	N	Y	0.222%
		Hoplitis	*producta* (Cresson)	B	Y	Y	Y	0.233%
			spoliata (Provancher)	B	Y	Y	N	0.207%
			truncata (Cresson)	B	N	N	Y	0.755%
		Osmia	*pumila* Cresson	B	Y	Y	Y	11.307%
			caerulescens (Linnaeus)	B	Y	Y	Y	10.455%
			lignaria Say	B	Y	Y	Y	0.648%
			atriventris Cresson	B	N	Y	N	0.170%
		Anthidium	***manicatum*** (Linnaeus)	B	Y	N	Y	0.015%
		Coelioxys	*alternata* Say	P (B)	Y	N	N	0.004%
			moesta Cresson	P (B)	N	Y	N	0.015%

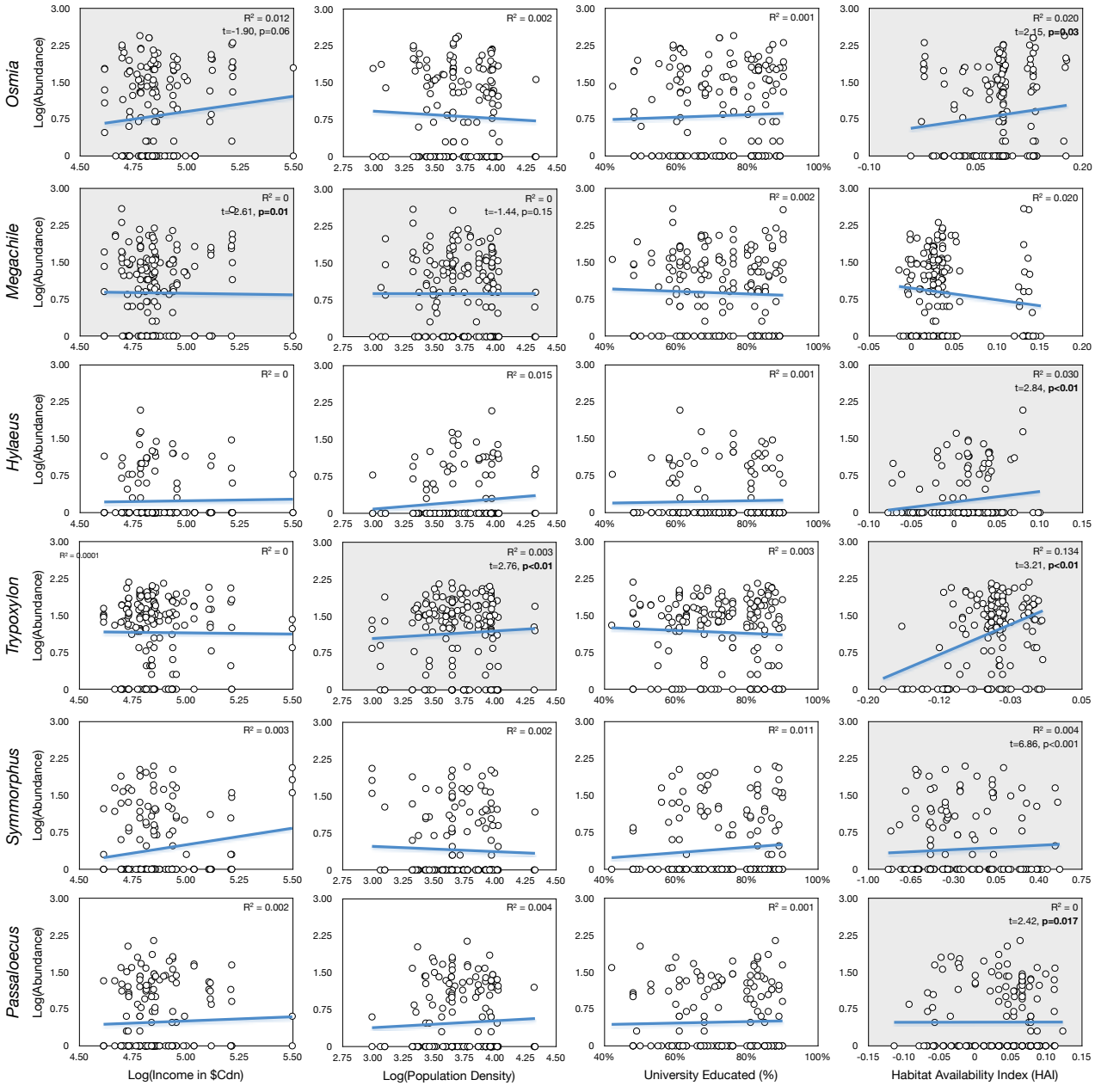
		sayi Robertson	P (B)	Y	Y	Y	0.019%
	Stelis	*lateralis* Cresson	P (B)	Y	Y	N	0.004%
		vernalis Mitchell	P (B)	N	Y	N	0.004%
Colletidae	*Hylaeus*	*affinis* Smith	B	Y	Y	Y	0.430%
		annulatus (Linnaeus)	B	Y	Y	Y	0.485%
		hyalinatus Smith	B	N	Y	Y	0.411%
		leptocephalus Morawitz	B	N	Y	Y	0.074%
		mesillae (Cockerell)	B	Y	N	Y	0.081%
		modestus Say	B	Y	Y	Y	0.033%
		punctatus Brullé	B	Y	Y	N	0.030%
		verticalis (Cresson)	B	N	Y	N	0.030%
Vespidae	*Ancistrocerus*	*adiabatus* (Saussure)	W	Y	Y	Y	0.774%
		antilope (Panzer)	W	Y	Y	Y	1.548%
		gazella (Panzer)	W	N	N	Y	0.085%
	Symmorphus	*canadensis* (Saussure)	W	Y	Y	Y	3.285%
		bifasciatus (Linnaeus)	W	N	N	Y	0.011%
		cristatus (Saussure)	W	Y	Y	Y	3.696%
		albomarginatus (Saussure)	W	Y	N	N	0.019%
	Euodynerus	*planitarsis* (Bohart)	W	Y	Y	Y	0.307%
		foraminatus (Saussure)	W	Y	Y	Y	1.130%
	Monobia	*quadridens* (Linnaeus)	W	Y	Y	Y	0.178%
Crabronidae	*Passaloecus*	***gracilis*** (Curtis)	W	Y	Y	Y	2.218%
		cuspidatus Smith	W	Y	Y	Y	0.793%
	Psenulus	***pallipes*** (Panzer)	W	Y	Y	Y	3.233%
	Trypoxylon	*frigidum* Smith	W	Y	Y	Y	11.007%
		collinum Smith	W	Y	Y	Y	8.992%
		lactitarse Saussure	W	Y	Y	Y	2.604%
Sphecidae	*Isodontia*	*mexicana* (Saussure)	W	Y	Y	Y	3.000%
Pompilidae	*Auplopus*	*mellipes* (Say)	W	Y	Y	Y	0.526%
	Dipogon	*sayi* Banks	W	N	Y	Y	0.052%
Leucospidae	*Leucospis*	*affinis* (Say)	P (W)	Y	Y	Y	0.026%
Eulophidae	*Melittobia*	*chalybii/acasta*	P (W)	Y	Y	Y	2.666%
Sapygidae	*Sapyga*	*centrata* Leconte	P (W)	Y	Y	Y	0.415%
		louisi Krombein	P (W)	Y	Y	Y	0.307%
Gasterupiidae	*Gasteruption*	***assectator*** (Linnaeus)	P (W)	Y	Y	Y	0.044%
Ichneumonidae	*Messatoporus*	***discoidalis*** (Cresson)	P (W)	Y	Y	N	0.011%

		Phytodietus	*vulgaris* Cresson	P (W)	Y	Y	Y	0.007%
		Perithous	***septemcinctorius*** (Thunberg)	P (W)	Y	N	N	0.004%
			divinator (Rossi)	P (W)	Y	Y	Y	0.133%
		Ephialtes	*manifestator* (Linnaeus)	P (W)	N	Y	Y	0.022%
		Campoplex	*sp. 1*	P (W)	N	Y	N	0.004%
		Hercus	*fontinalis* Holmgren	P (W)*	Y	Y	Y	0.019%
	Chalcididae	*Monodontomerus*	*obscurus* Westwood	P (W)	Y	Y	Y	0.100%
	Chrysididae	*Chrysis*	***angustula*** Schenck	P (W)	N	Y	N	0.004%
			cembricola Krombein	P (W)	Y	Y	Y	0.052%
			coerulans Fabricius	P (W)	Y	Y	Y	0.007%
		Caenochrysis	*doriae* (Gribodo)	P (W)	Y	Y	Y	0.030%
			tridens (Lepeletier)	P (W)	Y	Y	Y	0.333%
		Pseudomalus	*auratus* (Linnaeus)	P (W)	Y	Y	N	0.037%
			Sp. 1	P (W)	N	N	Y	0.004%
Diptera	Bombyliidae	*Anthrax*	*irroratus* Say	P	Y	Y	Y	0.037%
	Sarcophagidae	*Amobia*	*sp. +*	P	Y	Y	Y	0.530%
		Sarcophagid	*sp. 1*	P	Y	Y	Y	0.096%
	Conopidae	*Physocephala*	*marginata* (Say)	P	Y	Y	Y	0.022%
Coleoptera	Dermestidae	*Trogoderma*	*sp. 1*	P	Y	Y	Y	0.030%
	Meloidae	*Nemognatha*	*piazata* (Fabricius)	P	N	N	Y	0.007%
Strepsiptera	Stylopidae	*Paraxenos*	*bishoppi* (Pierce)	P	Y	N	N	0.004%
		Paraxenos	*smithii*	P	Y	Y	Y	0.159%
		Pseudoxenos	*sp. 1*	P	N	N	Y	0.007%

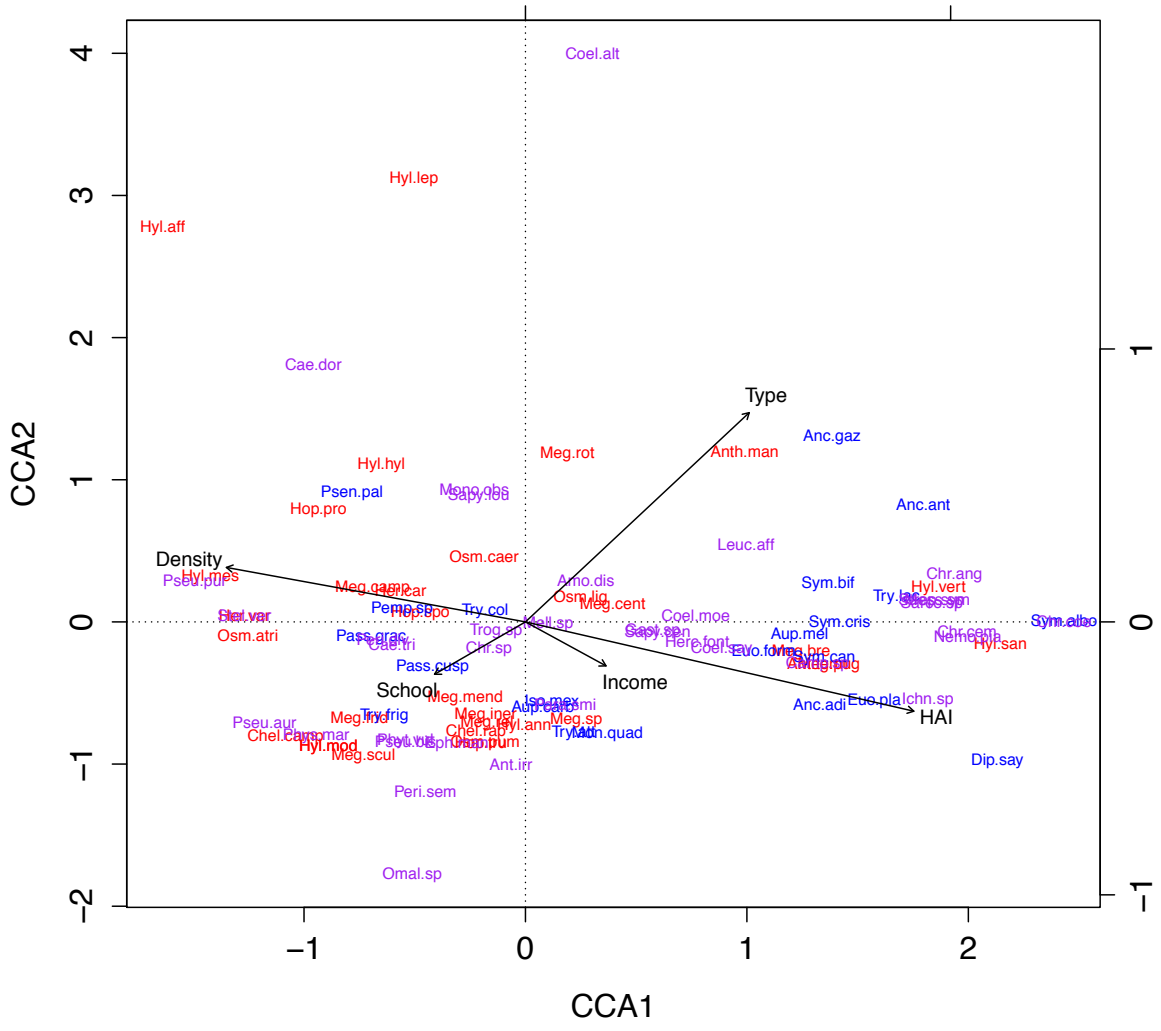
Appendix F. Socioeconomic factors that influence bee, wasp, and parasite species richness. Scatterplot boxes shaded grey included those factors that were identified in the top model equation for each colonizer group. A bolded p-value identifies those factors that had a significant effect on the observed data.



Appendix G. Socioeconomic factors affecting the three most common bee genera, *Megachile, Osmia,* and *Hylaeus,* and the three most common wasp genera, *Trypoxylon, Passaloecus,* and, *Symmorphus*, Scatterplot boxes shaded grey included those factors that were identified in the top model equation for each colonizer group. A bolded p-value identifies those factors that had a significant effect on the observed data.



Appendix H. A complete CCA biplot that ordinates all species identified from nest boxes in the study and their responses to variables including site type (“type”), habitat availability index (“HAI”), the mean household income (“income”), human population density (“density”), and the proportion of university educated households (“School”). Bees are labeled in red, nest provisioning wasps in blue, and all parasites in purple.



Appendix I. CCA loadings for CCA1 and CCA2 axes for each species included in the biplot.

Genus	Species	CCA1	CCA2
Anthophora	*terminalis* Cresson	1.319792779	-0.292859954
Megachile	*brevis* Say	1.245228359	-0.214693811
	campanulae (Robertson)	-0.690013267	0.23565736
	centuncularis (Linnaeus)	0.393419074	0.119754198
	frigida Smith	-0.75002939	-0.683068111
	inermis Provancher	-0.179672254	-0.651672746
	mendica Cresson	-0.272114879	-0.534196361
	pugnata Say	1.370892789	-0.301279126
	relativa Cresson	-0.173667803	-0.708386537
	rotundata Fabricius	0.189349376	1.182448826
	sculpturalis Smith	-0.732077776	-0.945374234
Heriades	*carinata* Cresson	-0.563501247	0.221007935
	variolosa (Cresson)	-1.268776333	0.04865663
Chelostoma	***campanularum*** (Kirby)	-1.083199679	-0.807091434
	rapunculi (Lepeletier)	-0.223219786	-0.773317156
Hoplitis	*producta* (Cresson)	-0.934855422	0.789715131
	spoliata (Provancher)	-0.474596825	0.062286305
	truncata (Cresson)	-0.200830598	-0.861120164
Osmia	*pumila* Cresson	-0.18225495	-0.852752566
	caerulescens (Linnaeus)	-0.186232528	0.462456432
	lignaria Say	0.248473408	0.170065599
	atriventris Cresson	-1.253379186	-0.096717785
Anthidium	***manicatum*** (Linnaeus)	0.989514002	1.199394694
Coelioxys	*alternata* Say	0.302983746	4.000874738
	moesta Cresson	0.768901719	0.049847141
	sayi Robertson	0.886324151	-0.192006018
Stelis	*lateralis* Cresson	-0.51149525	-1.776960558
	vernalis Mitchell	-1.268776333	0.04865663
Hylaeus	*affinis* Smith	-1.637817091	2.769480765
	annulatus (Linnaeus)	-0.005269079	-0.732659382
	hyalinatus Smith	-0.651389999	1.103371501
	leptocephalus Morawitz	-0.504160223	3.11268797
	mesillae (Cockerell)	-1.423386999	0.313147869
	modestus Say	-0.889880452	-0.883157734
	punctatus Brullé	2.144509407	-0.16298362
	verticalis (Cresson)	1.865399419	0.235531204
Ancistrocerus	*adiabatus* (Saussure)	1.329302038	-0.58122562
	antilope (Panzer)	1.796605119	0.825054654
	gazella (Panzer)	1.384632112	1.301643287
Symmorphus	*canadensis* (Saussure)	1.349708795	-0.250332076
	bifasciatus (Linnaeus)	1.366413865	0.268831386
	cristatus (Saussure)	1.419134807	-0.004078446
	albomarginatus (Saussure)	2.432393675	0.003345375
Euodynerus	*planitarsis* (Bohart)	1.574630893	-0.555726141
	foraminatus (Saussure)	1.076069161	-0.198944198
Monobia	*quadridens* (Linnaeus)	0.370833742	-0.788149721
Passaloecus	***gracilis*** (Curtis)	-0.696320625	-0.106497336
	cuspidatus Smith	-0.419857201	-0.317007183
Psenulus	***pallipes*** (Panzer)	-0.783336328	0.90601848
Trypoxylon	*frigidum* Smith	-0.637448787	-0.664642205

	collinum Smith	-0.181888625	0.078140584
	lactitarse Saussure	1.675042666	0.172157131
Isodontia	*mexicana* (Saussure)	0.119091437	-0.549995414
Auplopus	*mellipes* (Say)	1.238147428	-0.088192542
Dipogon	*sayi* Banks	2.130958995	-0.978779776
Leucospis	*affinis* (Say)	0.995936388	0.547084052
Melittobia	*chalybii/acasta*	0.102716967	-0.013757413
Sapyga	*centrata* Leconte	0.59683797	-0.078636588
	louisi Krombein	-0.210861118	0.890080798
Gasteruption	***assectator*** (Linnaeus)	0.583795914	-0.062507688
Messatoporus	***discoidalis*** (Cresson)	1.846251726	0.149680949
Phytodietus	*vulgaris* Cresson	-0.541724929	-0.837929171
Perithous	***septemcinctorius*** (Thunberg)	-0.451965227	-1.190297099
	divinator (Rossi)	-0.644394162	-0.125063298
Ephialtes	*manifestator* (Linnaeus)	-0.310102828	-0.855707736
Campoplex	*sp. 1*	1.319792779	-0.292859954
Hercus	*fontinalis* Holmgren	0.775995539	-0.134063657
Monodontomerus	*obscurus* Westwood	-0.230740557	0.932658037
Chrysis	***angustula*** Schenck	1.937159299	0.334211058
	cembricola Krombein	1.994611742	-0.06511176
	coerulans Fabricius	2.432393675	0.003345375
Caenochrysis	*doriae* (Gribodo)	-0.957522746	1.809515828
	tridens (Lepeletier)	-0.602378574	-0.155713506
Pseudomalus	*auratus* (Linnaeus)	-1.178044296	-0.708466094
	Sp. 1	-1.492469594	0.283155057
Anthrax	*irroratus* Say	-0.065349007	-1.004979931
Amobia	*sp. +*	0.272807319	0.291900642
Sarcophagid	*sp. 1*	1.834917847	0.127418242
Physocephala	*marginata* (Say)	-0.945058552	-0.804866321
Trogoderma	*sp. 1*	-0.132513007	-0.06635163
Nemognatha	*piazata* (Fabricius)	1.996836733	-0.114917579
Paraxenos	*bishoppi* (Pierce)	-0.541724929	-0.837929171
Paraxenos	*smithii*	0.179645607	-0.582573547
Pseudoxenos	*sp. 1*	1.846251726	0.149680949

Appendix J. Summary of model selection processes for each of the six bee species using Akiake's Information Criterion (AIC). Ψ denotes theprobability of a bee occupying a site when not detected, and *p* denotes the probability of being detected using a nest box when present at the site. The terms in parentheses indicate what factors are affecting each probability with a '.' indicating the probability is constant across all states. ΔAIC is the relative difference in AIC values, *w* is the AIC model weight, -2*l* is twice the negative log-likelihood and *K* is the number of parameters in the model. For all models the same structure was maintained for the detection-related component of the model.

Species	Model	AIC	ΔAIC	AIC weights	Model Likelihood	K	-2*LogLike
M. campanulae	Ψ(site),*p*(.)	411.33	0.00	0.4605	1.0000	2	407.33
	Ψ(foot,site),*p*(.)	412.05	0.72	0.3213	0.6977	3	406.05
	Ψ(.),*p*(.)	413.48	2.15	0.1572	0.3413	2	409.48
	Ψ(foot),*p*(.)	415.39	4.06	0.0605	0.1313	2	411.39
	Ψ(site),*p*(site)	428.00	16.67	0.0001	0.0002	2	424.00
	Ψ(foot),*p*(site)	428.02	16.69	0.0001	0.0002	2	424.02
	Ψ(.),*p*(site)	428.08	16.75	0.0001	0.0002	2	424.08
	Ψ(foot),*p*(foot,site)	428.77	17.44	0.0001	0.0002	3	422.77
	Ψ(foot,site),*p*(site)	429.37	18.04	0.0001	0.0001	3	423.37
	Ψ(foot,site),*p*(foot,site)	429.81	18.48	0.0000	0.0001	4	421.81
	Ψ(site),*p*(foot,site)	429.87	18.54	0.0000	0.0001	3	423.87
	Ψ(.),*p*(foot,site)	430.00	18.67	0.0000	0.0001	3	424.00
	Ψ(.),*p*(foot)	450.17	38.84	0.0000	0.0000	2	446.17
	Ψ(site),*p*(foot)	455.64	44.31	0.0000	0.0000	2	451.64
	Ψ(foot,site),*p*(foot)	457.27	45.94	0.0000	0.0000	3	451.27
	Ψ(foot),*p*(foot)	458.48	47.15	0.0000	0.0000	2	454.48

Species	Model	AIC	ΔAIC	AIC weights	Model Likelihood	K	-2*LogLike
O. pumila	Ψ(site),*p*(.)	456.96	0.00	0.5082	1.0000	2	452.96
	Ψ(foot,site),*p*(.)	458.84	1.88	0.1985	0.3906	3	452.84
	Ψ(.),*p*(.)	459.35	2.39	0.1538	0.3027	2	455.35
	Ψ(foot),*p*(.)	459.63	2.67	0.1337	0.2632	2	455.63

	Ψ(.),*p*(site)	468.89	11.93	0.0013	0.0026	2	464.89
	Ψ(site),*p*(site)	468.98	12.02	0.0012	0.0025	2	464.98
	Ψ(foot),*p*(site)	469.23	12.27	0.0011	0.0022	2	465.23
	Ψ(.),*p*(foot,site)	470.84	13.88	0.0005	0.0010	3	464.84
	Ψ(site),*p*(foot,site)	470.86	13.90	0.0005	0.0010	3	464.86
	Ψ(foot,site),*p*(site)	470.91	13.95	0.0005	0.0009	3	464.91
	Ψ(foot),*p*(foot,site)	471.23	14.27	0.0004	0.0008	3	465.23
	Ψ(foot,site),*p*(foot,site)	472.85	15.89	0.0002	0.0004	4	464.85
	Ψ(.),*p*(foot)	481.31	24.35	0.0000	0.0000	2	477.31
	Ψ(foot,site),*p*(foot)	483.02	26.06	0.0000	0.0000	3	477.02
	Ψ(site),*p*(foot)	485.37	28.41	0.0000	0.0000	2	481.37
	Ψ(foot),*p*(foot)	488.53	31.57	0.0000	0.0000	2	484.53

Species	Model	AIC	ΔAIC	AIC weights	Model Likelihood	K	-2*LogLike
M. pugnata	Ψ(foot,site),*p*(site)	89.51	0.00	0.9098	1.0000	3	83.51
	Ψ(foot,site),*p*(foot)	96.90	7.39	0.0226	0.0248	3	90.90
	Ψ(foot),*p*(foot,site)	96.91	7.40	0.0225	0.0247	3	90.91
	Ψ(foot),*p*(site)	97.00	7.49	0.0215	0.0236	2	93.00
	Ψ(foot),*p*(.)	97.97	8.46	0.0132	0.0146	2	93.97
	Ψ(foot,site),*p*(foot,site)	98.72	9.21	0.0091	0.0100	4	90.72
	Ψ(.),*p*(foot)	105.12	15.61	0.0004	0.0004	2	101.12
	Ψ(.),*p*(.)	105.57	16.06	0.0003	0.0003	2	101.57
	Ψ(.),*p*(site)	105.69	16.18	0.0003	0.0003	2	101.69
	Ψ(.),*p*(foot,site)	107.12	17.61	0.0001	0.0001	3	101.72
	Ψ(foot,site),*p*(.)	109.26	19.75	0.0000	0.0001	3	103.26
	Ψ(site),*p*(foot)	109.83	20.32	0.0000	0.0000	2	105.83
	Ψ(site),*p*(site)	110.45	20.94	0.0000	0.0000	2	106.45
	Ψ(site),*p*(.)	110.80	21.29	0.0000	0.0000	2	106.80
	Ψ(site),*p*(foot,site)	111.83	22.32	0.0000	0.0000	3	106.83
	Ψ(foot),*p*(foot)	256.22	166.71	0.0000	0.0000	2	252.22

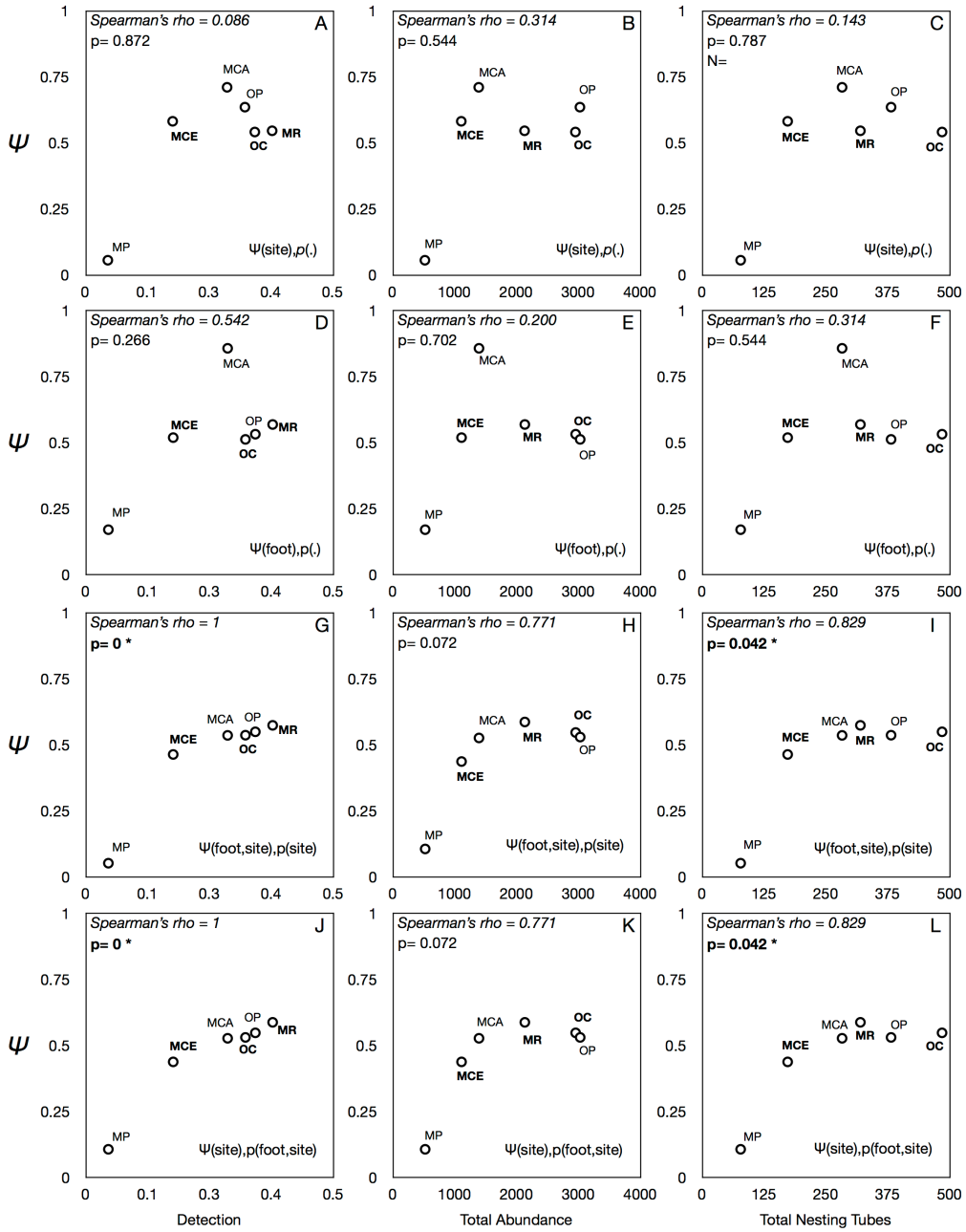
Species	Model	AIC	ΔAIC	AIC weights	Model Likelihood	K	-2*LogLike
M. rotundata	Ψ(site),*p*(foot,site)	468.79	0.00	0.3536	1.0000	3	462.79

	Ψ(.),*p*(foot,site)	469.58	0.79	0.2382	0.6737	3	463.58
	Ψ(foot),*p*(foot,site)	470.36	1.57	0.1613	0.4561	3	464.36
	Ψ(foot,site),*p*(foot,site)	470.55	1.76	0.1467	0.4148	4	462.55
	Ψ(site),*p*(site)	474.03	5.24	0.0257	0.0728	2	470.03
	Ψ(foot),*p*(site)	474.10	5.31	0.0249	0.0703	2	470.10
	Ψ(.),*p*(site)	474.74	5.95	0.0180	0.0510	2	470.74
	Ψ(foot,site),*p*(site)	475.26	6.47	0.0139	0.0394	3	469.26
	Ψ(foot),*p*(.)	476.89	8.10	0.0062	0.0174	2	472.89
	Ψ(.),*p*(.)	477.37	8.58	0.0048	0.0137	2	473.37
	Ψ(site),*p*(.)	477.65	8.86	0.0042	0.0119	2	473.65
	Ψ(foot,site),*p*(.)	478.68	9.89	0.0025	0.0071	3	472.68
	Ψ(.),*p*(foot)	494.20	25.41	0.0000	0.0000	2	490.20
	Ψ(site),*p*(foot)	494.45	25.66	0.0000	0.0000	2	490.45
	Ψ(foot,site),*p*(foot)	496.05	27.26	0.0000	0.0000	3	490.05
	Ψ(foot),*p*(foot)	500.30	31.51	0.0000	0.0000	2	496.30

Species	Model	AIC	ΔAIC	AIC weights	Model Likelihood	K	-2*LogLike
O. caerulescens	Ψ(site),*p*(foot,site)	474.12	0.00	0.2523	1.0000	3	468.12
	Ψ(.),*p*(foot,site)	474.17	0.05	0.2461	0.9753	3	468.17
	Ψ(foot),*p*(foot,site)	474.27	0.15	0.2341	0.9277	3	468.27
	Ψ(foot,site),*p*(foot,site)	475.17	1.05	0.1493	0.5916	4	467.17
	Ψ(.),*p*(.)	478.39	4.27	0.0298	0.1182	2	474.39
	Ψ(foot),*p*(.)	479.03	4.91	0.0217	0.0859	2	475.03
	Ψ(site),*p*(.)	479.04	4.92	0.0216	0.0854	2	475.04
	Ψ(site),*p*(site)	480.36	6.24	0.0111	0.0442	2	476.36
	Ψ(.),*p*(site)	480.45	6.33	0.0107	0.0422	2	476.45
	Ψ(foot),*p*(site)	480.53	6.41	0.0102	0.0406	2	476.53
	Ψ(foot,site),*p*(.)	480.85	6.73	0.0087	0.0346	3	474.85
	Ψ(foot,site),*p*(foot)	482.20	8.08	0.0044	0.0176	3	476.20
	Ψ(site),*p*(foot)	493.40	19.28	0.0000	0.0001	2	489.40
	Ψ(.),*p*(foot)	494.10	19.98	0.0000	0.0000	2	490.10
	Ψ(foot,site),*p*(foot)	495.39	21.27	0.0000	0.0000	3	489.39
	Ψ(foot),*p*(foot)	499.51	25.39	0.0000	0.0000	2	495.51

Species	Model	AIC	ΔAIC	AIC weights	Model Likelihood	K	-2*LogLike
M. centuncularis	Ψ(foot),*p*(.)	287.52	0.00	0.3172	1.000	2	283.52
	Ψ(site),*p*(.)	287.74	0.22	0.2842	0.8958	2	283.74
	Ψ(.),*p*(.)	288.02	0.50	0.2470	0.7788	2	284.02
	Ψ(foot,site),*p*(.)	289.38	1.86	0.1252	0.3946	3	283.38
	Ψ(.),*p*(site)	293.63	6.11	0.0149	0.0471	2	289.63
	Ψ(.),*p*(foot,site)	295.55	8.03	0.0057	0.0180	3	289.65
	Ψ(site),*p*(site)	297.91	10.39	0.0018	0.0055	2	293.91
	Ψ(foot),*p*(site)	297.99	10.47	0.0017	0.0053	2	293.99
	Ψ(site),*p*(foot, site)	299.74	12.22	0.0007	0.0022	3	293.74
	Ψ(foot,site),*p*(site)	299.78	12.26	0.0007	0.0022	3	293.78
	Ψ(foot),*p*(foot,site)	299.82	12.30	0.0007	0.0021	3	293.82
	Ψ(foot,site),*p*(foot,site)	301.74	14.22	0.0003	0.0008	4	294.74
	Ψ(.),*p*(foot)	311.42	23.90	0.0000	0.0000	2	307.42
	Ψ(foot,site),*p*(foot)	318.22	30.70	0.0000	0.0000	3	312.22
	Ψ(site),*p*(foot)	319.75	32.23	0.0000	0.0000	2	315.75
	Ψ(foot),*p*(foot)	332.91	45.39	0.0000	0.0000	2	328.91

Appendix K. Rank correlations of species detection, abundance, and number of nesting tubes colonized against occupancy estimates for all species derived from the top four model equations as determined by AIC applied to each species individually (see Table 6). Plots A-C show results for Ψ estimates from model equation Ψ(site),*p*(.)), D-F is Ψ(foot),*p*(.)), G-I is Ψ(site),*p*(foot,site)), J-L is Ψ(foot,site),*p*(site)). An asterisk indicates significance at the α=0.05 level.



Appendix L. List of public talks on urban bees and their needs given during my PhD.

Date	Talk	Location	Organization	Attend
Jul 2015	High Park's Native Bees	Toronto	High Park Naturalists	50
Jun 2015	David Suzuki Foundations Got Milkweed? Campaign's action for pollinators	Toronto	West Toronto Railpath Stewards	50
Jun 2015	Wild Bees Q and A	Toronto	Rosedale Public School	25
Apr 2015	Bees in the garden	Toronto	Pape Ave Jr Public School	50
Mar 2015	Trap-nesting wild bees and wasps	Etobicoke	Etobicoke Master Gardeners	40
Feb 2015	Cavity-nesting bees in Toronto	Toronto	Foodshare	100
Oct 2014	Green Roof Research in Canada	Ottawa	Tremco Company	120
Oct 2014	Bees in the urban landscape	Port Dover	Port Dover Master Gardeners	60
Jun 2014	Wild bees in the City	Toronto	Environics	40
Jun 2014	Cosmopolitan Bees	Toronto	East York Community Garden	15
May 2014	Toronto's Wild Bees	Etobicoke	Plantworld	45
Aug 2013	Wild Bees: Ecology and Diversity	Toronto	Rouge Park Conservation Authority	60
Jul 2013	Toronto's Wild Bees	Toronto	Cowan-Masyrnk Community Garden	20
Jun 2013	Cavity-nesting bees and bee hotels.	Toronto	High Park Nature Centre	25
Jun 2013	Cavity-nesting bee hotels	Pickering	TDSB Insurance Group	20
May 2013	Wild bees	Toronto	Black Creek Urban Farm	25
May 2013	Determinants of urban cavity-nesting bees.	Toronto	Green Neighbours 21	25
May 2013	Bees in Toronto	Toronto	Rose Avenue Public School	50
Apr 2013	Habitat for wild bees	Toronto	Bartley St. Permaculture Centre	25
Mar 2013	Toronto's Wild Bees	Toronto	Parkview Community Garden	20
Sept 2012	Overwintering Bees in the Garden	Toronto	Toronto Botanical Gardens	15
Aug 2012	Wild Bees: Ecology and Diversity	Toronto	Rouge Park Conservation Authority	60
Jul 2012	How to build a bee nest box	Toronto	Toronto Botanical Gardens	15
Jul 2012	Toronto's Wild Bees	Toronto	Cowan-Masyrnk Community Garden	50
June 2012	Toronto's Wild Bees	Toronto	High Park Nature Centre	30
May 2012	Bees in Toronto	Toronto	Rose Avenue Public School	60
Apr 2012	Wild bees	Toronto	Pegasus Homeschool Group	25
Dec 2011	Bees in Toronto	Toronto	Ralph Thorton Centre Homeschool Group	30
Aug 2011	Wild Bees: Their ecology and diversity	Toronto	Rouge Park Conservation Authority	60
May 2011	Bees in Toronto	Toronto	Humewood Public School	20
April 2011	Cavity-nesting bees in urban gardens	Toronto	East York Community Garden	15

Appendix M. RESEARCH ARTICLE: Pollen specialization by solitary bees in an urban landscape.

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1. Abstract

Many polylectic bee species are known to specialize locally on one or a few pollen types to increase foraging efficiency. What is relatively unknown is how different landscapes influence foraging decisions, and whether habitat alteration, such as that resulting from urbanization, influences broad-scale foraging activities of bees. This study evaluates the type and diversity of pollen collected by two solitary bees that are common in Toronto, Ontario, Canada, the native *Osmia pumila* and the exotic *O. caerulescens*, sampled in trap nests set up in urban parks and gardens. We found that the dominant pollen in every successful brood cell was either of one widespread, cosmopolitan lawn-invasive plant species (*Trifolium repens*) or one of two wind-pollinated tree genera (*Quercus* spp. and *Betula* spp.). In combination, these three represented more than 90% of all pollen collected by each bee species. Despite considerable overlap in the dominant pollen types collected by each bee species, the exotic *O. caerulescens* was significantly more specialized than the native *O. pumila*. Brood cells with *Betula* as the dominant pollen type were more pollen species-rich than those cells having *Trifolium* or *Quercus* as dominant, perhaps a result of the comparatively low protein content in *Betula* pollen.

2. Introduction

Many species of bee possess traits that permit their survival in urban landscapes. Elucidating these traits is an important field of study for predicting how fragmentation and other anthropogenic disturbances alter species assembly (Niemelä et al. 2000) and pollination services (Williams et al. 2010). Cities are model landscapes for investigating the effects of

fragmentation and anthropogenic disturbance, both of which vary in intensity and frequency, usually increasing towards the urban core (McDonnell et al. 1997). In urban areas, the majority of bee species recorded are polylectic, collecting pollen and nectar from a variety of native and exotic, ornamental, and invasive flowering plants, shrubs, and trees (Matteson et al. 2008). Despite many studies evaluating the diversity of wild bees in urban and suburban landscapes (Tommasi et al. 2004; Smith et al. 2006; Fetridge et al. 2008; Banaszak-Cibicka & Żmihorski, 2011), none has assessed pollen use by urban bees. Analyzing and identifying pollen grains from nests provides a more useful record of the floral host use over an extended period of time than does floral observations in the field (Cane & Sipes, 2006), and acknowledging these relationships can have implications in sustaining native pollinators and pollination services (Kearns & Inouye, 1997; Jones & Jones, 2001; Fontaine et al. 2006; Müller et al. 2006; Bosch et al. 2009; Ollerton et al. 2011).

In cities, knowledge of pollen, nectar, and nesting requirements of bees is important for advancing the integration of ecology into landscape design in support of plant-pollinator assemblages (Cane, 2005). This is important because urbanization and the associated loss of vegetation have been shown to generally have a negative effect on bee populations (Zanette et al. 2005; Winfree et al. 2009). At the same time, citizens are becoming increasingly engaged in socio-economic activities requiring pollination, such as wildlife gardening and urban agriculture (Smit & Nasr, 1992; Drescher, 2004). This could include selecting combinations of plant species that provide floral resources all season, which is particularly important for social bees active all season (Pleasants, 1980), while also fulfilling other important city planning criteria such as canopy cover and shading using flowering trees (Dwyer et al. 1992). Indeed, many large-scale urban re-forestation and vegetation initiatives are underway. In New York, an initiative of PlaNYC is to re-vegetate the boroughs with one million planted trees by 2017 (Rosenthal & Brechwald, 2013). Another initiative in the city of Toronto aims to double the tree canopy cover

from 17% to 34% by 2050 (City of Toronto, 2007). In these reforestation plans, canopy-providing tree selection has the potential to modify, either positively or negatively, the activity of non-target, pollen-dependent insects (Dreistadt et al. 1990).

Members of the solitary bee genus *Osmia* (Hymenoptera: Megachilidae) are often common in urban landscapes (Tommasi et al. 2004; Evaraars et al. 2011). Many *Osmia* are polylectic, with each female constructing its own nest after mating in spring and early summer (Cripps & Rust, 1989). The success of *Osmia* may be mediated in part by flexibility in nest selection, and the availability of accidental human-made nesting sites. Many *Osmia* will build their nests in woody or non-woody plant stems, branches, or logs, but also holes drilled into building material such as wooden boards, brick, or mortar, and even intentionally bundled nests of cardboard paper tubes or reeds (Krombein, 1967; Free & Williams, 1970; Sheffield et al. 2008; Mader et al. 2010). An *Osmia* nest consists of a gallery of brood cells, each cell provisioned with pollen and nectar produced, in sequence, from the back of the nest to the front. Each cell is lined with masticated leaves and/or mud and the same material is usually used to plug the entrance to the gallery when complete (Cane et al. 2007).

The developmental success of *Osmia* larva is unaffected by the richness of pollen provisioned, with brood able to develop successfully on even a single pollen type (Williams & Tepedino, 2003). Such specialization presumably minimizes time spent foraging (Raw, 1974; Strickler, 1979; Chittka et al. 1999; Müller et al. 2006) while simultaneously reducing rates of parasitism through decreasing the duration of absences from the nest (Goodell, 2003). Specialization in this case would particularly increase the efficiency of brood provisioning in the springtime, when there are fewer foraging alternatives and weather conditions are less stable (Radmacher & Strohm, 2010). Like adaptive specialization of foraging behaviour in suboptimal weather, bees that can specialize on pollen in less predictable or fragmented environments might have greater population persistence in city landscapes.

In this study we investigate the pollen diversity and preference of one native, *O. pumila*, and one exotic, *O. caerulescens*, bee species to determine whether pollen use by *Osmia* in a city landscape is consistent with observations of pollen specialization by *Osmia* in naturalized (Raw, 1974; Cripps & Rust, 1989; Rust, 1990; Kraemer & Favi, 2005) and orchard agricultural landscapes (Torchio, 1976; Vicens & Bosch, 2000). Further, since pollen collection by exotic solitary bees is poorly known (Goulson, 2000), the study will examine differences between the co-occurring native and exotic species.

3. Methods

Sampling

From May to October 2011, 190 trap nests were set up in the city of Toronto in private gardens, community gardens, green roofs, and parks. Each trap nest was constructed from a 30 cm piece of recyclable PVC piping of 10 cm diameter with one end fitted with a pipe cap, the other with a faceplate bearing 30 cardboard tubes (Custom Paper Tubes, Cleveland, OH), 10 of each of three different widths (3.4mm, 5.5mm and 7.6mm) that were plugged at the capped end of the pipe. Once recovered, all cardboard tubes were opened and the contents analyzed. Average trap nest colonization was 33.6% with *O. pumila* and *O. caerulescens* representing 16.7% and 10.3% of the total sample, respectively.

Pollen analysis

Osmia pumila and *O. caerulescens* were identified and 20 galleries containing *O. pumila* and 11 containing *O. caerulescens* were selected so to best reflect the entire sampling area (Figure A5). This resulted in 160 successful *O. pumila* brood cells from 10 nesting locations and 58 successful *O. caerulescens* brood cells from 7 locations (see Figure A5). Pollen was collected from each of these brood cells from the frass that is excreted just prior to pupation (Raw, 1974;

Davidson & Evans, 2010). Each frass-pollen sample was transferred to a slide with two drops of water and pulverized with the blunt end of a spatula, followed by a thorough mixing and re-distribution on the slide with an insect mounting pin (Teper, 2007). The spatula was cleaned between each slide preparation and a fresh mixing pin was used each time to avoid contamination among samples. Pollen was then air-dried for 60 minutes, and a drop of glycerin and a drop each of fuschsin and methyl green in 70% ethyl alcohol were added to each sample to make the pollen microstructure more visible for identification (Raw, 1974; Kearns & Inouye, 1997). All pollen grain samples are preserved and placed in storage at the Packer Collection at York University, Toronto, Canada.

Pollen grains from each of the prepared samples were examined using a Canon E05 40D camera with a K2 lens and a 10x lens attachment and photographed using a Microoptics ML 1000 fiberoptics illuminating system at the highest flash setting and highest magnification. Photographs of several fields of view (moving 2x above and 2x below the original magnification) were taken. The images were uploaded to Adobe Photoshop Lightroom 3 and exported to Helicon Focus 5.2 x 64, which compiles multiple fields of view of a single location to provide a composite image with a greater depth of field. Data were obtained from each of a minimum of three locations on the slide in an attempt to ensure that at least 600 pollen grains (maximum 200 per slide location) could be identified in each sample.

Pollen grains were identified to genus because of the difficulties associated with a finer taxonomic assessment; this level has been shown to be sufficient for examining pollen specialization (Eltz et al. 2001; Radmacher & Strohm, 2010). Pollen identities were determined using keys in McAndrews et al. (1973) and Crompton & Wojtas (1993). Pollen grains that made up less than 1% of the total count were considered contaminants (Eltz et al. 2001), or as having been haphazardly collected while bees were foraging for nectar (Radmacher & Strohm, 2010) and omitted from analysis.

Statistical Analysis

Average pollen richness was calculated as the average number of pollen grain types both within a brood cell and within a nesting gallery for each *Osmia* species. Pollen grain specialization was calculated per brood cell, gallery, and trap nest location using Levins' standardized measure of niche breadth (B_n) (Feinsinger et al. 1981). A B_n value nearing 1 reflects higher specialization on a single pollen type and values approaching 0 represent increasing breadth of pollen species collection. A Welch's two-sample t-test ($\alpha = 0.05$) (assuming unequal variance) was used to compare the number of brood cells per gallery constructed, pollen richness per gallery, and pollen specialization between the two species. A linear regression analysis tested whether specialization within a gallery of each species were associated with an increase in the number of brood cells constructed by an individual, since specialization has been shown to increase productivity in oligolectic bees (Strickler, 1979). Finally, an analysis of variance with a Tukey HSD post-hoc analysis was used to detect significant differences in the dominance of pollen grain types in the brood cells between the two species. All statistics were completed using R version 2.15.2 (R Foundation for Statistical Computing, 2012).

4. Results

The native *O. pumila* collected significantly more pollen types (n = 8) than the non-native *O. caerulescens* (n = 6) ($t_{29} = -2.59$, $p = 0.015$) and was significantly less specialized on the dominant pollen it collected compared to the non-native *O. caerulescens* ($t_{15} = 2.42$, $p = 0.029$). That said, high specialization was noted in both species, with instances in which 100% of the pollen mass was of a single pollen type (3% of all brood cells). Moreover, 79% of *O. caerulescens* cells were provisioned with >95% (by proportion) of a single host species compared to only 37% of *O. pumila* cells. Despite the difference in pollen specialization, the number of brood cells per gallery was not significantly different between species ($t_{22} = -0.466$, p

= 0.646), nor was there any effect of specialization on the number of brood cells produced within *O. pumila* (p = 0.862) or *O. caerulescens* (p = 0.389).

Both bee species shared a surprisingly similar diet breadth, concentrating primarily on White Clover, *Trifolium repens* (Fabaceae), and two wind-pollinated tree genera: Oak (likely *Quercus rubra* and/or *Quercus alba*), and Birch (likely *Betula papyrifera* and/or *Betula alleghaniensis*) (Figure A6). Clover pollen was the dominant grain type in 75% of *O. pumila* and 54% of *O. caerulescens* galleries, followed by Oak dominant in 15% for *O. pumila*, 27% for *O. caerulescens*, and Birch (10% for *O. pumila*, 9% for *O. caerulescens*). Interestingly, when Birch was dominant in a brood cell of *O. caerulescens*, the proportion of other co-occurring pollen types was proportionally significantly greater than when either Clover or Oak was dominant (F = 5.75, p = 0.025) (Figure A7). Pollen was also collected in small amounts (<5% each) from Willow (likely *Salix discolor, Salix nigra,* and/or *Salix alba*), Maple (likely *Acer saccharum*, *Acer saccharinum*, and/or *Acer platanoides*), Cherry (*Prunus* spp.), Vetch (likely *Vicia sativa*), and Dandelion (*Taraxacum officinale*).

5. Discussion

In this study, we find that two solitary bees abundant in an urban landscape exhibit high pollen specialization on wind-pollinated trees (*Quercus* spp., *Betula* spp.) and on a nitrogen-fixing legume common in pastures and now an abundant lawn-invading cosmopolitan weed (*Trifolium repens*). *Trifolium repens* has a near worldwide distribution and is common in urban areas (Turkington & Burdon, 1983). Having a moderately high protein content (35.4%) (Roulston et al. 2000), it is visited by many bee species including both *O. pumila* (Goodell, 2003) and *O. caerulescens* (Hennig & Ghazoul, 2011). The other two primary pollen types collected by both bee species were from predominantly wind-pollinated trees: Oak (*Quercus*) and Birch (*Betula*). Wind-pollinated trees are not reliant on insect pollination but provide an abundant source of

pollen for bees (Molina et al. 1996). The pollen of Oak, like White Clover, contains a relatively high proportion of protein (38.8%), but Birch contains much less, approximately 28% (Roulston et al. 2000). Although there is no evidence that bees assess the nutritional content of pollen while foraging (Roulston & Cane, 2000), low protein content may have resulted in both Birch being only the third most commonly collected pollen and, when used, to be associated with a greater species richness of pollen sources than the other two main pollen sources. Similarly, in related bee genera, Praz et al (2008) found that species specializing on pollen having low protein content were more flexible in their use of pollen from different plant families.

The City of Toronto's Urban Forestry department commonly specifies both Oak and Birch for landscaping and reforestation projects (City of Toronto, 2012). These trees, along with Willow and Maple, which were found in some *Osmia* cells in this study, bear easily accessible pollen concentrated on catkins having many small open flowers with little or no corolla (Giovanetti & Aronne, 2011). With large trees permeating the urban landscape, each having potentially many thousands of flowers in a single season, these species might prove locally significant resources for pollen collecting insects within the urban matrix, potentially increasing connectivity in fragmented habitat (Ricketts, 2001).

Our results reflect those of other studies examining pollen loads of *Osmia* in less urban environments. In particular, in rural England, Raw (1974) found 83% of the pollen provisioned in opened brood cells of *O. caerulescens*, *O. rufa*, and *O. leaiana* came from the combination of a wind-pollinated tree (*Quercus* spp.) and a lawn weed (*Ranunculus* spp.). Another study on a suburban university campus in Germany found 38.8% of all brood cells of *O. bicornis* contained >95% of a single pollen type, most often the wind-pollinated *Quercus* or the partially wind-pollinated *Acer* (Maple) (Radmacher & Strohm, 2010). In our study, both *O. pumila* and *O. caerulescens* specialized on one of each of the three dominant pollen types (*Trifolium, Quercus,* and *Betula*) all of which are widespread in the city. It is evident that inherent local pollen

specialization by polylectic bees on one or a few grain types might reflect a trait suited for persistence in urban landscapes. In this case, specialization on whichever dominant grain is found in the neighbourhood would ensure foraging success in these increasingly novel environments.

Different from other investigations of pollen collection by *Osmia* that examined native species only (e.g. Raw, 1974; Cripps & Rust, 1989; Radmacher & Strohm, 2010) we report that pollen collection by the exotic bee species *O. caerulescens*, was significantly more specialized than the co-occurring native, *O. pumila*. Although little is known about host plant restrictions of solitary bees in non-native habitats, Goulson (2000) notes that two introduced bees, *Apis mellifera* and *Bombus terrestris*, visit a greater diversity of floral hosts when outside their native range. The significantly greater specialization on a single pollen type by *O. caerulescens* could reflect differences in dietary requirements or preference between species, or that *O. caerulescens* is more restricted in its pollen collection in a non-native habitat. Despite the difference in degree of specialization, there was no apparent effect of specialization on the number of brood cells provisioned by the two species. Specialization by oligolectic bees has been suggested to increase foraging efficiency and the number of brood cells that can be constructed within a given season (Strickler, 1979; Chittka et al. 1999). Although not examined in this study, it is possible that for some bee species, visiting more different types of flowers may not equate to a significant increase in foraging efficiency and brood provisioned because of diverse pollen resources in managed parks and in home and community gardens.

Conclusion

From analyzing pollen extracted from the frass of brood provisioned in trap nests set up throughout the city of Toronto, the native *O. pumila* and exotic *O. caerulescens* were found to specialize on the pollen collected to provision their brood. Further, the exotic species was

significantly more specialized in foraging than the co-occurring native. The dominant pollen grains for both species were from that of a grass-invading cosmopolitan weed, *T. repens*, and two wind-pollinated tree genera, *Quercus* and *Betula*. No specialization by either *Osmia* species was found to occur on entomophilous native plants, or crops significant for urban agriculture; furthermore it remains unknown whether specialization on abundant cosmopolitan weeds and wind-pollinated trees limits pollination of remnant native plants and crops in urban landscapes.

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7. Figures

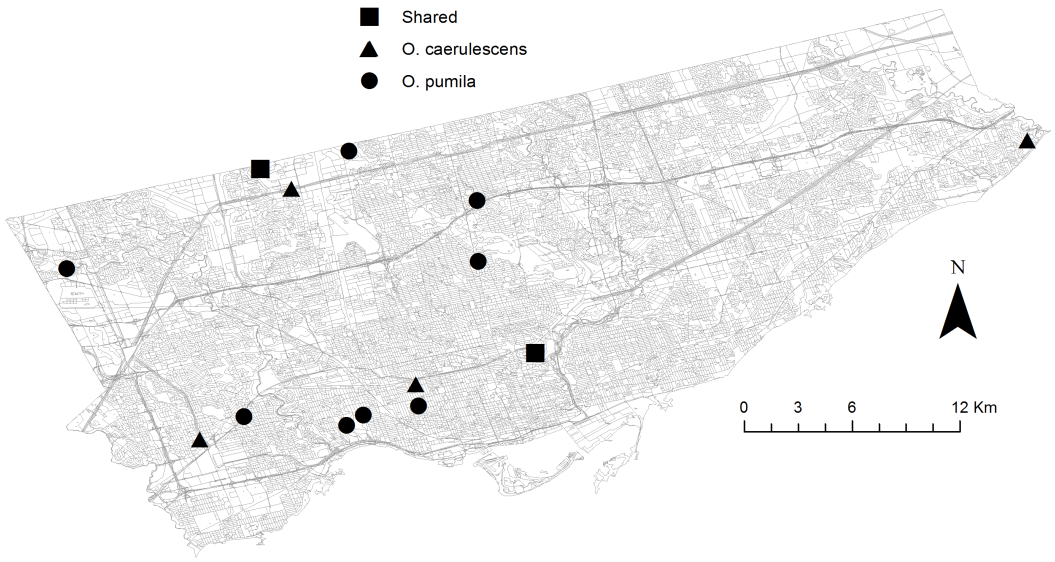

Figure A5. Map of study site localities in and around Toronto, Ontario, Canada, created using ArcGIS 10 software (ESRI, Toronto, Canada). Open areas and City parks and recreation land are highlighted in green. One sampling site located north of the city boundary is omitted from the map.

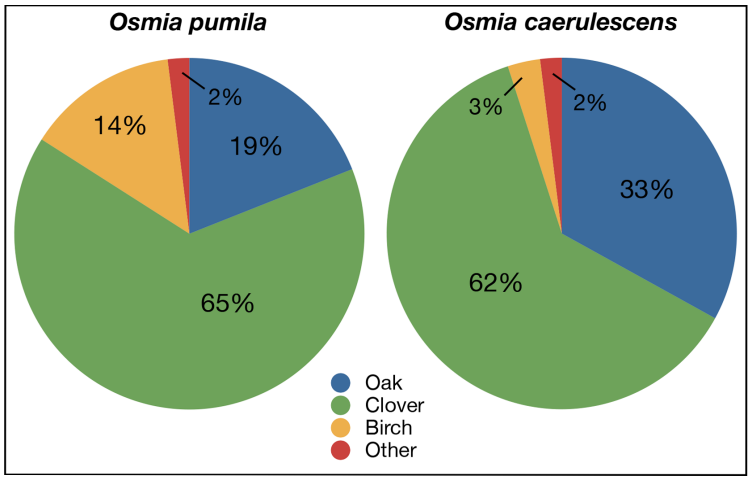

Figure A6. Total proportion of each of the specialized pollen types collected by *O. pumila* and *O. caerulescens*.

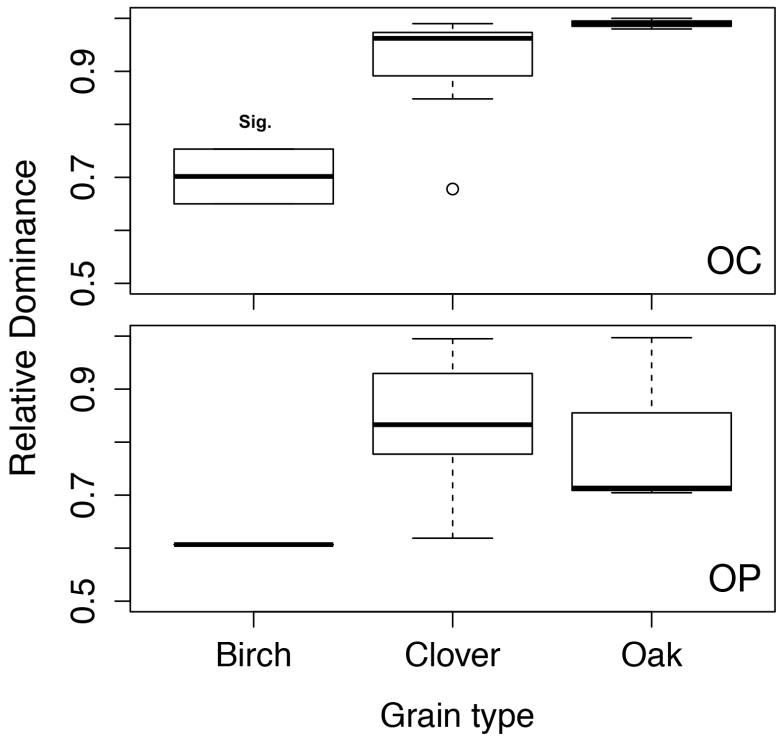

Figure A7. A boxplot for each commonly collected pollen genera, demonstrating the difference between their relative dominance when they are the dominant grain in the brood cells of either *O. caerulescens* (OC) and *O. pumila* (OP). A post-hoc Tukey HSD analysis revealed that Oak (p-adjusted = 0.02) and Clover (p-adjusted = 0.05) were significantly more dominant than Birch in brood cells of *O. caerulescens* (Birch denoted with a “Sig.” to mark significance), but no difference was evident for *O. pumila*.

Appendix N. RESEARCH ARTICLE: Bee species-specific nesting material attracts a generalist parasitoid: Implications for co-occurring bees in nest box enhancements

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1 Abstract

Artificial nests (e.g., nest boxes) for bees are increasingly being used to contribute to nesting habitat enhancement for bees that use preexisting cavities to provision brood. They usually incorporate additional nesting materials that vary by species. Cavity-nesting bees are susceptible to brood parasitoids that recognize their host(s) using visual and chemical cues. Understanding the range of cues that attract parasitoids to bee nests, including human-made analogues, is important if we wish to control parasitism and increase the potential value of artificial nests as habitat-enhancement strategies. In this study, we investigated the cues associated with the orientation of the generalist brood parasitoid *Monodontomerus obscurus* Westwood (Hymenoptera: Torymidae) to the nests of a common cavity-nesting resin bee *Megachile campanulae* (Robertson) (Megachilidae). The parasitoids were reared from previously infested *M. campanulae* brood cells and placed into choice trials where they were presented with pairs of different nest material cues. Among different materials tested, we found that *Mo. obscurus* was most attracted to fresh resin collected directly from *Pinus strobus* trees followed by previously used resin collected from the bee nest. The parasitoid also attacked other bee species in the same nest boxes, including those that do not use resin for nesting. Our findings suggest that *M. campanulae* could act as a magnet, drawing parasites away from other bee hosts co-occurring in nest boxes, or, as an attractant of *Mo. obscurus* to nest boxes, increasing attacks on co-occurring host bee species, potentially undermining bee diversity enhancement initiatives.

2. Introduction

Bee pollinator habitat enhancement in urban landscapes has become a focal activity in scientific research and in citizen engagement to promote local environmental issues, including pollinator decline (Gaston et al. 2006; Hernandez et al. 2009). One strategy to enhance pollinator habitat has been to use cavity-nesting bee nest boxes made of holes drilled in wood, hollow plant stems or paper tubes bound together. These nest boxes are used by a wide range of bee, and wasp, species that nest in pre-existing cavities (e.g., Krombein, 1967; Cane et al. 2007; Sheffield et al. 2012; Rightmeyer et al. 2013). Brood cells are provisioned in a linear series from the back to the front of the nesting cavity, and are lined with extraneous materials that vary by taxa (Cane et al. 2007; Litman et al. 2011). Artificial nest boxes have been used widely in ecological research (e.g. Tepedino, 1988 Tscharntke et al. 1998, Tylianakis et al. 2006; Sheffield et al. 2008a; Zurbuchen et al. 2010; MacIvor et al. 2014) and implemented to augment pollinator numbers in agroecosystems (Bohart, 1972; Bosch & Kemp 2002; Sheffield et al. 2008b). Although nest boxes may be a valuable nesting resource for solitary bees when natural nest sites are limited, such aggregation may increase the search effectiveness of cleptoparasites (consume food provisioned for host; host usually killed), parasitoids (parasites that kill their host), and predators (attack and consume host) (Rosenheim, 1990; Wcislo, 1996). Cavity-nesting bees have been suggested to suffer less from parasitism than ground nesters because natural enemies have to search in a three-dimensional environment to find nests in plant material whereas the soil surface is more two-dimensional (Michener, 1985). With most nest box designs, the aggregation of many potential nest sites in a small area may facilitate the functional and numerical responses (Holling, 1966) of natural enemies of bees. However, nest boxes in which hosts co-occur with non-hosts might confuse natural enemies and reduce their search efficiency; as well, the defensive behaviours of aggregated bees might contribute to the protection of neighbouring hosts (Rosenheim, 1990). Artificial nest boxes could also facilitate

selfish herding in bees, in which hosts seek cover among other potential hosts or non-hosts to reduce their chances of attack by natural enemies (Hamilton, 1971). It is clear that artificial habitat augmentation methods such as bee nest boxes have the potential of becoming population sinks instead of sources.

Cavity-nesting bees are hosts to a wide range of cleptoparasites, parasitoids, and predators (Krombein, 1967). These orient to and recognize oviposition opportunities based on visual, tactile and chemical cues produced by the host, by the host's nesting material (Vinson, 1976; Matthews et al. 2009), or floral elements (e.g. oils) (Pekkarinen et al. 2003). Brood parasitoids in the genus *Monodontomerus* (Hymenoptera: Chalcidoidea: Torymidae) for example, find and enter nests of the host bee then oviposit into bee larvae (Krombein, 1967; Tepedino, 1988). Several to dozens of the parasitoid can emerge from a single host and, because of their short generation times, offspring of the original attacking female can parasitize other host brood within the same nest box (Eves, 1970; Tepedino, 1988). Good design could reduce parasitism in artificial nest boxes; however, bundling nests together, as occurs in most nesting block designs, might be more to the benefit of the parasitoids than the hosts which are more susceptible to attack (Bosch, 1992; Wcislo, 1996). Understanding the factors that influence parasitism rates in nest boxes is important if this alternative pollinator management strategy and marketable product is to be used effectively.

Despite being common through much of eastern North America, the resin bee, *Megachile* (*Chelostomoides*) *campanulae* (Robertson) is poorly studied compared to many other megachilid bees. Females provision brood cells in holes in wood but will readily accept nest boxes as an alternative. *Megachile campanulae* brood cells are lined with resin collected from pine (*Pinus* spp.) trees. The bee is attacked by the parasitoid *Monodontomerus obscurus* Westwood, a generalist attacking many bee species (Grissell, 2000). An investigation of host recognition of another cavity-nester, *Osmia cornuta* (Latreille) (Megachilidae) by the congeneric

parasitoid *Mo. aeneus* (Fonscolombe) determined that volatiles emitted from cocoons and frass were the primary attractants (Filella et al. 2011). *Osmia cornuta* uses mud to partition brood cells (Bosch, 1994), while *M. campanulae* uses pine resins. Pine aromatics have been shown to attract wasp parasitoids to sawfly oviposition sites (Hilker et al. 2002) and thus could be attractive to parasitoids in other Hymenopteran host-recognition interactions. This study aimed to investigate whether the resins used by *M. campanulae* are attractive to *Mo. obscurus*. *Monodontomerus obscurus* was reared from *M. campanulae* brood cells collected from nest boxes and presented with choices of materials from hosts nests as well as pine resin collected fresh from trees.

3. Methods

Parasitoid and Host Rearing

Nest boxes (Figure A8A) were used to sample cavity-nesting bees in Toronto and surrounding regions, among which both *M. campanulae* (identified using Sheffield et al. 2012) and *Mo. obscurus* (identified by Dr. Gary Gibson at the Canadian National Collection, Ottawa, Ontario) were collected. Voucher specimens are stored at the Packer Collection at York University (PCYU) in Toronto, Canada. Each nest box consisted of thirty paper tubes, 15cm long and of three different widths (10 of each: 3.4mm, 5.5mm, 7.6mm) inserted into a 30cm piece of 10cm width white PVC pipe. These were set up on wooden stakes or on low-lying tree branches at 192 locations in the city of Toronto from early May to late October 2012 and 200 sites during the same period in 2013. *Megachile campanulae* is active from April to September over most of its range (Mitchell, 1962) and readily took to the nest boxes, provisioning brood cells almost exclusively in the 5.5mm diameter tubes. In October in each sampling year, nest boxes were collected and opened, then *M. campanulae* brood cells dissected to determine whether they were parasitized by *Mo. obscurus* (Figure A8B). In both 2012 and 2013 parasitized brood cells

were stored individually in cells in 24-well assay trays, in a cold room at 4°C, then removed and reared to adulthood in a growth chamber at 26°C and 55-60% humidity the following year. Two to four days post-emergence, the naïve (never having experienced a host as an adult), *Mo. obscurus* adults were grouped by natal host brood cell for entry into choice experiments.

Host Cue Choice Experiments

Upon emergence, *Mo. obscurus* groups were randomly assigned to one of five different two-choice treatments so that each pairwise treatment combination had four trials. This approach resulted in a variable number of *Mo. obscurus* among trials. We chose not to try to make these numbers equal in each case because the wasps are too easily damaged in handling and we did not want to further reduce our sample size. The two-choice assays were conducted in large rectangular arenas (30cm x 13.5cm x 7cm) made almost entirely of fine mesh to ensure adequate airflow. These are comparable to arenas used in similar experiments (Stireman, 2002; Carpita et al. 2012; Benelli et al. 2013) including those on host cue use by other parasitoid wasps (Silva-Torres et al. 2005). In each choice treatment, two *M. campanulae* nest components were hidden inside of two separate 3cm long sections of 5.5mm width cardboard nesting tube (Custom Paper Tubes, Cleveland, OH) that were each attached at a 90° angle to the centre of a 5cm x 2 cm strip of yellow sticky trap tape (Safer's brand) at opposite ends of the choice arena. A single group of *Mo. obscurus* was added to each arena just after the sticky tape containing the two choices were set, by placing a single opened 1.5ml eppendorf tube containing one group into the centre of the arena. Each eppendorf tube was oriented directly perpendicular to both treatment types so wasps emerging were not biased in the direction they move leaving the tube, then the mesh lid of the arena was sealed. To reduce any effect of light in orienting *Mo. obscurus*, the growth chamber (26°C and 50-55% humidity during the trials) in which the study was conducted was windowless and all lights turned off for the duration of each

choice experiment, each trial lasting three hours. Since *Mo. obscurus* groups did not emerge all at once but rather over a two-day period, it was possible to conduct only one trial at a time in the growth chamber, with all trials being completed over a five-day period in 2013, and a three-day period in 2014. To eliminate odours from the previous treatment, a new arena was used for every replicate of each treatment and to minimize any positioning effects, the choice materials within the same treatment were assigned to different ends in each replication.

From the 2012 population, we tested the attractiveness of four different *M. campanulae* nest elements: (1) used resin (UR) collected from the cells having been in contact with cocoon and frass elements (some fragments presumably embedded), (2) resin collected fresh from *Pinus strobus* trees (TR) located at the York University campus (43°46'28.55"N, 79°30'10.31"W), (3) *M. campanulae* larvae (L), and (4) Polyurethane-based adhesive sealant (P) (Dap, Polyurethane Sealant, Baltimore, MD) which has a similar consistency to the resin used and in 2012 was found in a *M. campanulae* cell series in place of the resins normally collected (MacIvor & Moore 2013). From the 2013 populations, more pairwise combinations were tested, including (5) cardboard nesting tubes without materials or larva that represented nest controls in the absence of cues. All pairwise combinations are shown in Figure A9.

Choice was determined by the proportion of *Mo. obscurus* females in each group entered into each treatment entrapped by the sticky tape associated with each of the attractants after the allotted time period had passed. Any dead or undecided specimens were excluded from the study. A Welch's unpaired two tailed t test was used in R version 2.15.2 (R Foundation for Statistical Computing, 2012) to determine attractiveness of each *M. campanulae* nest element to *Mo. obscurus* females only and both sexes combined.

4. Results

From the 2012 field season, of 452 *M. campanulae* brood cells from 51 nesting tubes at 16 sites, *Mo. obscurus* parasitized 29 brood cells at 5 sites (31.3%) accounting for 6.4% of all host cells. In 2013, 473 *M. campanulae* brood cells from 70 nesting tubes at 19 sites were recorded, with *Mo. obscurus* parasitizing only 18 *M. campanulae* brood cells at 4 sites (21.1%) accounting for 3.8% of all host cells. *Megachile campanulae* was the dominant host of *Mo. obscurus*, which also emerged from nesting tubes containing four other megachilid bees: *M. rotundata* (Fabricius) (2012+2013)*, Osmia pumila* Cresson (2012), *O. caerulescens* (Linnaeus) (2012+2013), and *Heriades carinata* Cresson (2012+2013). In both years, *Megachile campanulae* provisioned, on average, 7.65±0.88 brood cells per cell series and in parasitized nest galleries, *Mo. obscurus* occupied 58.2±11.0% of brood cells. Of those *Mo. obscurus* emerging from the host brood cells, on average, 51.0±4.6% survived and were available for use in choice trials. The mean number of individual *Mo. obscurus* entered into trials was 7.1+/-3.2 of which 21.3% were male (2012 only) [female biased sex ratios are common in this species (Eves, 1970) as well as others in the genus (Hamilton, 1967)].

Resin fresh from *Pinus strobus* trees (TR) was significantly more attractive to the parasitoids than host larvae alone (L) (♀ only: t=2.872, df=6, p=0.028, ♀+♂: t=3.676, df=6, p=0.001) and polyurethane plastic (P) used as a nesting material substitute by *M. campanulae* (♀ only: t=3.196, df=6, p=0.02, ♀+♂: t=3.938, df=6, p=0.01) (Figure A10). Resin collected fresh from trees was somewhat more attractive than used resin from nests (UR) (♀ only: t=1.355, df=6, p=0.221, ♀+♂: t=0.917, df=6, p=0.395), however UR was only slightly more attractive than P as nesting substrate control (♀ only: t=1.90, df=6, p=0.11, ♀+♂: t=1.824, df=6, p=0.120) and larva alone (♀ only: t=3.590, df=6, p=0.016, ♀+♂: t=2.507, df=6, p=0.046) (Figure A10). Similarly, attraction to the polyurethane based window sealant (P) control was no different from that of the larvae alone (♀ only: t=0.91, df=6, p=0.400, ♀+♂: t=1.810, df=6, p=0.130). In 2013,

no-choice trials (e.g. nesting tubes set up without any materials or larva) representing the absence of cues found many *Mo. obscurus* stuck to sticky tape, but no significant choice for one direction or the other (♀ only: t=2.110, df=6, p=0.07, ♀+♂: t=3.492, df=6, p=0.06).

5. Discussion

Efforts to counteract pollinator decline have caught the imagination of the general public and has contributed to production and marketing of numerous artificial nest box designs now commercially available. However, it has yet to be determined whether such nest boxes serve to augment pollinator populations or act as sinks by rendering their occupants more susceptible to the aggregation of natural enemies such as cleptoparasites and parasitoids. Factors determining the effectiveness of host recognition by parasitoids in a broad sense have been extensively studied (Chesson & Murdoch, 1986; Hawkins, 2005). Yet there remains much work to be done in identifying the host cues that attract natural enemies to cavity-nesting bees in nest boxes. In our study, choice experiments revealed that resins, fresh from the tree or to a lesser extent that already used by bees is attractive to the generalist brood parasitoid, *Mo. obscurus*. Used resin from brood cells – having been in contact with frass and cocoons in the nest – was less attractive than resin directly from *Pinus strobus* trees. Frass and cocoon fragments were most attractive to *Mo. aeneus* in a similar study of a host (*O. cornuta*) that uses mud rather than resin (Filella et al. 2011). In contrast, we found parasitoids to be preferentially attracted to the fresh, and presumably more aromatic, resin. This suggests that the wasps will be attracted to nests that are actively being constructed by hosts rather than those from the previous year. Nesting materials vary considerably among cavity-nesting megachilid bee species (Horne, 1995; Cane et al. 2007; Litman et al. 2011), thus generalist parasites such as *Mo. obscurus* presumably can detect cues both common among a range of host species as well as other cues that are host species specific (Vinson, 1976). Generalist nest parasites like *Mo. obscurus* likely

have several means of detecting and orienting to potential hosts. In nest boxes in which several bee species co-occur, a generalist parasite may need only one cue, such as aromatic tree resins, to orient to the nest box, at which point it perceives information about other less easily detectable cavity-nesting bee species that are equally suitable as hosts.

Monodontomerus wasps have been reported to parasitize many bee species in the cavity-nesting genera *Osmia* (e.g. Vicens et al. 1994; Tschartcke et al. 1998; Grissell, 2000; Strohm, 2002; Bosch & Kemp, 2002) and *Megachile* (e.g. Eves, 1970; Tepedino, 1988; Grissell, 2000; Filella et al. 2011). Although *M. campanulae* was the primary host, an examination of the wider community of bees sampled in the nest boxes in this study revealed *Mo. obscurus* also parasitized *M. rotundata* (see Eves, 1970), *O. pumila*, *O. caerulescens*, and *H. carinata* (Table A4). *Monodontomerus obscurus* is not known from the later three hosts, but has been identified from the nests of several other *Osmia* species (Noyes, 2013). Three of the bees, *M. rotundata*, *O. caerulescens* and *H. carinata* were parasitized when *M. campanulae* co-occurred in the same nest box (Table A4). For co-occurring non- *M. campanulae* bees, success may be impacted by *Mo. obscurus* that are attracted to the nest box by the resinous nests of *M. campanulae*. Especially since nest building activity of all these species overlap in the study area and *Mo. obscurus* appeared to be most attracted to fresh resin (Figure A10). However, the proportion of brood cells parasitized in co-occurring non-*M. campanulae* species was much lower, suggesting bees that co-occur with *M. campanulae* may avoid attack by *Mo. obscurus* by 'seeking cover' in the presence of a more attractive host (*M. campanulae*) (Hamilton, 1971; Rosenheim, 1990). Evidence is limited in this study though, since the proportion of non-*M. campanulae* brood parasitized in the absence of *M. campanulae* was as low as when the bees co-occurred with *M. campanulae*. Nonetheless, these findings demonstrate there is a need to better understand relative attractiveness of different cavity-nesting bees to generalist parasitoids

and whether mixed species aggregations increases the chances of attack for species that might usually not be attractive to certain parasitoids.

Data resulting from the monitoring of bee populations and their parasites can be used to indicate regional environmental quality (Tscharntke et al. 1998; Frankie et al. 1998; Zayed et al. 2004; Zayed & Packer, 2005; Sheffield et al. 2013). Artificial nest boxes are useful in this regard because they are less prone to sampler bias, and data on cavity-nesting bees sampled passively can be used to extrapolate information that reflects the entire bee community (Westphal et al. 2008). As artificial nest boxes increasingly become part of pollinator enhancement strategies and set up by interest groups and concerned citizens, more is needed to understand the potential effects of nest boxes on local cavity-nesting bee and wasp communities and their natural enemies.

Conclusions

Our experiments show that *Mo. obscurus* parasitoids are attracted to the pine tree resins collected by *M. campanulae*, and that the parasitoid potentially uses the resins to locate host bee larvae. Although not significant, fresh resin from trees (TR) attracted more parasitoids than used resin (UR) collected from *M. campanulae* brood cells constructed in the previous year. Both TR and UR were significantly more attractive than the host larvae alone and TR significantly more attractive than polyurethane plastic (P) controls. Aggregated nesting among two or more cavity-nesting bee species is presumed to increase in landscapes in which artificial nest boxes are deployed. Understanding which cues augment parasite attractiveness to nest boxes may be essential to prevent them from becoming sink habitat rather than their intended use as support for wild bee biodiversity.

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7. Tables

Table A4. For non-*Megachile campanulae* bee hosts parasitized by *Mo. obscurus*, the number of sampling sites where parasitism occurred, the total number of host brood cells at those sites, and the proportion (%) of them parasitized by *Mo. obscurus* is shown for when (A) *M. campanulae* co-occurs and has at least one *Mo. obscurus* parasitized brood cell, (B) *M. campanulae* is present in the nest box but parasite-free, or (C) *M. campanulae* is absent.

	(A) present and parasitized	(B) present and parasite-free	(C) absent
Megachile rotundata (Fabricius)	0	1 site, 11 cells (18.2%)	3 site, 181 cells (7.7%)
Osmia pumila Cresson	0	0	2 sites, 9 cells (11.1%)
Osmia caerulescens (Linnaeus)	0	1 site, 31 cells (6.5%)	2 site, 53 cells (7.5%)
Heriades carinata Cresson	1 site, 35 cells (11.4%)	1 site, 16 cells (6.3%)	0

8. Figures

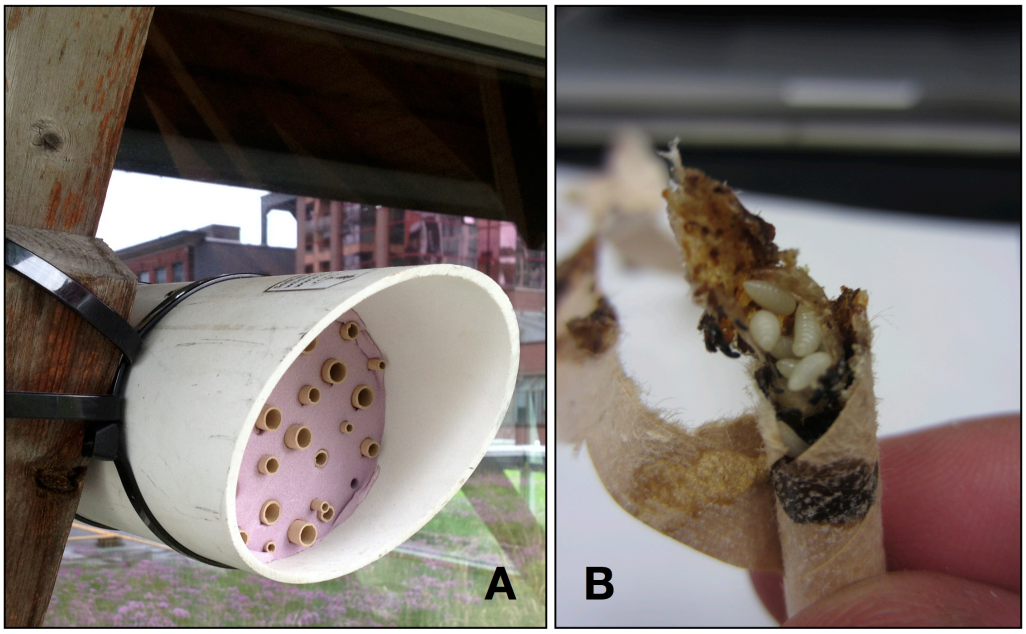

Figure A8. (A) The nest box design used in the study to collect *Megachile campanulae* and (B) a brood cell parasitized by *Monodontomerus obscurus* larvae

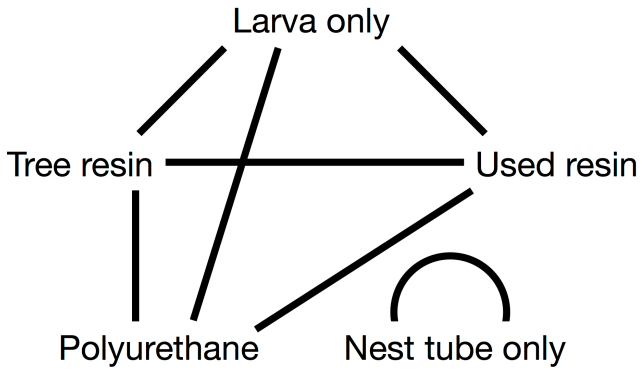

Figure A9. A diagram denoting all seven different two choice combination treatments (four trials per pair) of nesting elements used to examine the attractiveness of *Monodontomerus obscurus* to *Megachile campanulae* brood cells.

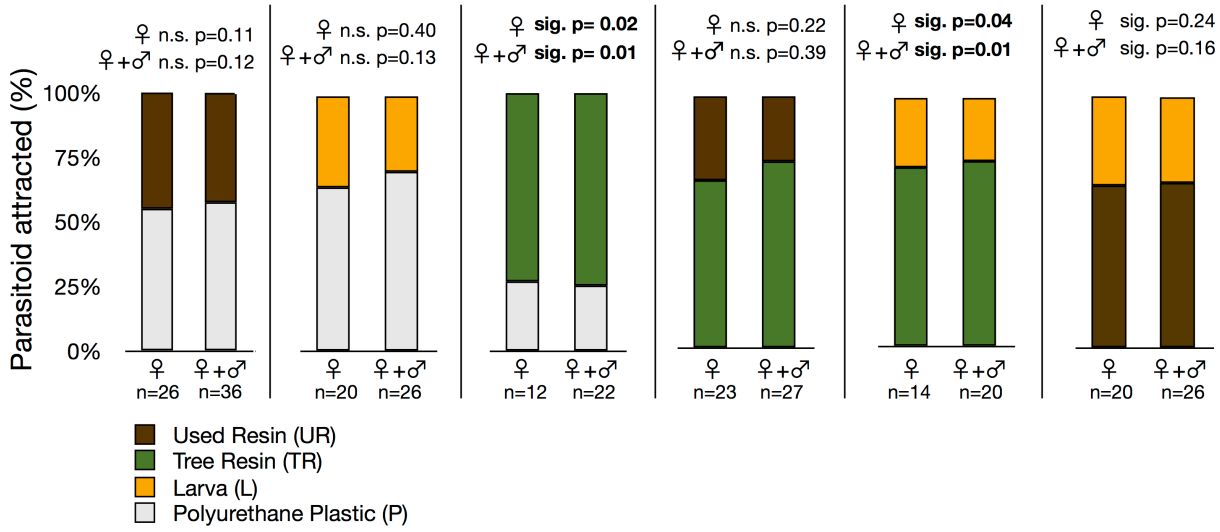

Figure A10. Barplots showing the proportion of parasitoids attracted to the different materials presented in two-choice experiments.

Appendix O. RESEARCH ARTICLE: Bees collect polyurethane and polyethylene plastics as novel nest materials

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1. Abstract

Plastic waste pervades the global landscape. Although adverse impacts on both species and ecosystems have been documented, there are few observations of behavioral flexibility and adaptation in species, especially insects, to increasingly plastic-rich environments. Here, two species of megachilid bee are described independently using different types of polyurethane and polyethylene plastics in place of natural materials to construct and close brood cells in nests containing successfully emerging brood. The plastics collected by each bee species resembled the natural materials usually sought; *Megachile rotundata*, which uses cut plant leaves, was found constructing brood cells out of cut pieces of polyethylene-based plastic bags, and *Megachile campanulae*, which uses plant and tree resins, had brood cells constructed out of a polyurethane-based exterior building sealant. Although perhaps incidentally collected, the novel use of plastics in the nests of bees could reflect ecologically adaptive traits necessary for survival in an increasingly human-dominated environment.

2. Introduction

Urbanization and other forms of human caused land use change can alter both the diversity and behavior of wild species (Slabbekoorn & Peet, 2003, Winfree et al. 2009). Flexibility in adapting to selective pressures exerted in these landscapes that are different from those arising in natural areas enables some species to persist over others (Yeh & Price, 2004, Shochat et al. 2006). One trait potentially indicative of a successful urban species is the recognition and novel use of

human made products to enhance foraging or nesting opportunities. With more novel material accumulating in the landscape the chance some will act as analogues to natural materials might result in their incidental, but successful use by animal species. Although not easily determined, novel uses of human made materials might result in an adaptive advantage, leading to more widespread use after multiple successful occurrences in a given population. Bowerbirds (Passeriformes: Ptilonorhynchidae) are one example that, in order to stand out during courtship, decorate nests with human-made products of specific colors (Diamond, 1986). Additionally, house sparrows (*Passer domesticus*) and house finches (*Carpodacus mexicanus*) have been reported to use discarded nicotine-laden cigarette butts in their nests that reduce ectoparasites (Suarez-Rodrıguez et al. 2012). One pervasive human-made compound common in all landscapes is plastic waste. Plastics are made to be strong, durable, and cheap, and as such are discarded as trash once used but resistance to degradation causes their accumulation in the natural landscape (Barnes et al., 2009). Plastics concentrate in landfills but also disperse across large areas in all habitat types, persisting in some cases for decades. Microorganisms and fungi have been studied colonizing or consuming them (Mergaert & Swings, 1996, Barratt et al. 2003), and both altricial (e.g., robins, sparrows, pigeons) and precocial (e.g., geese, swans) birds have been documented using plastics as materials in nest building. Few other examples of animals using plastics in place of natural nestbuilding resources have been recorded and that by insects is almost non-existent. One observation made over 50 years ago noted the stingless bee *Tetragonula hockingsi* Cockerell (Apidae: Meliponinae) collecting fresh house paint as it dried, presumably for use as nesting material (Medler, 1966).

The materials collected or secreted to construct brood cells and close a nest vary considerably by bee species. The majority of bees in the family Megachilidae collect materials from the landscape ranging from muds and small pebbles, to different plant leaves, stems, and resins (Michener, 2007, Cane et al. 2007). One species in particular, *Megachile* (Eutricharaea)

rotundata (Fabricius) (Hymenoptera: Megachilidae) is known to bring back a plethora of different natural materials, including cut leaves and flower petals (Hobbs, 1967, Mader et al. 2010). The bee is Eurasian in origin and introduced to our study region, arriving in North America some time in the mid-1930s (Stephen & Torchio, 1961; Cane, 2003) and soon after managed as an alternative pollinator (Bohart, 1972). Other megachilids, such as *Megachile* (Chelostomoides) *campanulae* (Robertson) (Hymenoptera: Megachilidae) collect plant resins in place of cut leaves (Krombein, 1967). Unlike *M. rotundata*, this species is native to Southern Ontario (Sheffield et al. 2011). In this paper, we describe the use of polyurethane and polyethylene-based products as alternatives to natural plant-based nesting materials by these two bee species. *Megachile rotundata* was discovered using pieces of polyethylene-based plastic shopping bags and M. campanulae used a polyurethane-based exterior house sealant. Both of these bees provision brood above ground in cavities such as holes in wood, or plant stems, or in pre-excavated holes in anthropogenic structures such as fences, awnings, brick walls, and human-made trap nests (Mader et al. 2010).

3. Methods

Trap nests were set up in Toronto in 2012 for research investigating urban landscape factors influencing bee populations. See MacIvor et al. (2014) for methodological details. Cavity-nesting bees use trap nests as alternatives to natural nesting locations where brood cell series are laid in a row, from the back of a pre-excavated nesting hole to the front. These nesting galleries were opened, brood cells inspected, and larvae reared to adults individually in a walk-in growth room where temperature (26°C) and humidity (65%) were controlled. It was during inspection of the nesting tubes we discovered non-natural materials built into the nests of two different bee species.

One brood cell series constructed by *Megachile campanulae* contained 7 brood cells (#1–7 from back to front), two of which (#4, #5) was made of a whitish green material of a less-gluey consistency than the natural nest material (Figure A11). An FTIR spectroscopy analysis with a Bruker Hyperion 1000 infrared microscope attached to a Tensor 27 FTIR Spectrometer were used to examine the material and a natural resin reference sample. These were analyzed directly by spreading on a potassium chloride window then compared with other reference materials including polyurethane polymers. An elemental analysis was done in a Hitachi S-4500 Field Emission Scanning Electron Microscope at 15 kv using a Quartz XOne x-ray microanalysis system. The samples were analyzed directly, without any coating.

A second cell series, constructed by *Megachile rotundata*, had 8 brood cells (#1–8 from back to front). Three of the cells were partially constructed with fragments of plastic bag, replacing on average 23% of the cut leaves in each cell. The first was cell #5 and 4 of 17 pieces were plastic, #6 had 3 of 15, and #7 had 4 of 16 (mean number of leaves in non-plastic containing cells was 16). All pieces were of the same white glossy color and ‘ plastic bag’ consistency and thus presumably from the same source (Figure A12).

4. Results & Discussion

Of the two polyurethane-based brood cells provisioned by *Megachile campanulae*, one (cell #4) was parasitized by the generalist brood parasite, *Monodontomerus obscurus* Westwood (Hymenoptera: Torymidae) (7 individuals emerged [4 female, 3 male]), and a female *M. campanulae* emerged from the second (cell #5). This bee species is common throughout Toronto, occupying 13.8% of all sites in 2011 and 8.6% in 2012 (polyurethane-containing cells amounting to only 0.74% of all cells collected). The FTIR spectroscopy analysis demonstrated that the unknown sample from the *M. campanulae* nest most closely resembled polyurethane polymers (Fig. 1). The X-ray microanalysis further supported this by revealing that Calcium (Ca),

Titanium (Ti), and Iron (Fe) were present in the material, each of these being common elements in polyurethane-based sealants and caulking (3M Company, 2012) (Figure A11C). Polyurethane-based sealants are commonly applied to the exteriors of all forms of buildings. Resin providing plants and trees are also common in the city in forested areas, home gardens, and in municipal landscape design. Since natural resins were found in the nesting cell series both in behind and in front of the plastic material, the use of polyurethanebased sealants might be incidental and not due to a lack of natural resin options.

Megachile rotundata was the most common bee surveyed in trap nests in both sampling years. The bee occupied 18.0% of all sites in 2011 and 19.9% of sites in 2012. Brood cells partially constructed with fragments of polyethylene based plastic bags represented 0.85% of all brood cells constructed. All were males and emerged successfully, parasite-free. The mandibular teeth markings in the cuts along the plastic bag nesting fragments were noticeably coarser and less uniform than those made in leaves from the same brood cell (Figure A12), suggesting the use of plastic bags represented an aberrant behavior. Dried juices and pulp created from the chewing of leaf pieces by megachilid bees contribute to them attaching together to form each cell (Trostle & Torchio, 1994). This natural process was presumably lost when the plastic pieces were used as they did not adhere to the other leaf pieces that comprised the cells, and easily flaked off when inspecting the brood cell architecture. Furthermore, since plastic pieces were found in combination with leaves in brood cells, and found only near the end of the cell series, bee naivete does not appear to be the cause for the use of plastic. The fact that *M. rotundata* returned to collecting leaves to finish the brood cells after using plastic suggests that leaf nesting materials were not limiting. It is interesting to note that in both bee species, the type of plastic used structurally reflects the native nesting material, suggesting that nesting material structure is more important than chemical or other innate traits of the material.

There may be some advantage in using plastic as a nesting material, as it might physically impede parasites infecting a recognized host. Stephen & Every (1970) noted that *Megachile rotundata* constructing cell series in plastic drinking straws were free of *Monodontomerus* parasitoids, which were unable to sting through the plastic wall; however up to 90% of brood were lost to mold because plastic inhibited diffusion of moisture. Certainly, polyurethane and polyethylene based plastics could also be a detriment to brood survival. Although this too was not evident in the study as all specimens survived to adulthood after artificial rearing in the lab, many other examples of plastics inhibiting essential functions including mobility, foraging, and respiration in other animals is documented (Barnes et al. 2009).

Our understanding of how plastics spontaneous integrate into natural ecological processes will increase as more human-made material and products build up in both urban and non-urban landscapes. Even more so, as ecologists, naturalists, and all hobbyists having access to a camera and Internet can quickly disseminate unique observations, which can be used to both engage the public, and contribute to empirical research (Silvertown, 2009). The extent to which humanmade products such as plastic become a fixed part of the landscape might act as a novel selective pressure further delineating urban adaptive and urban-avoiding species and subpopulations.

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6. Figures

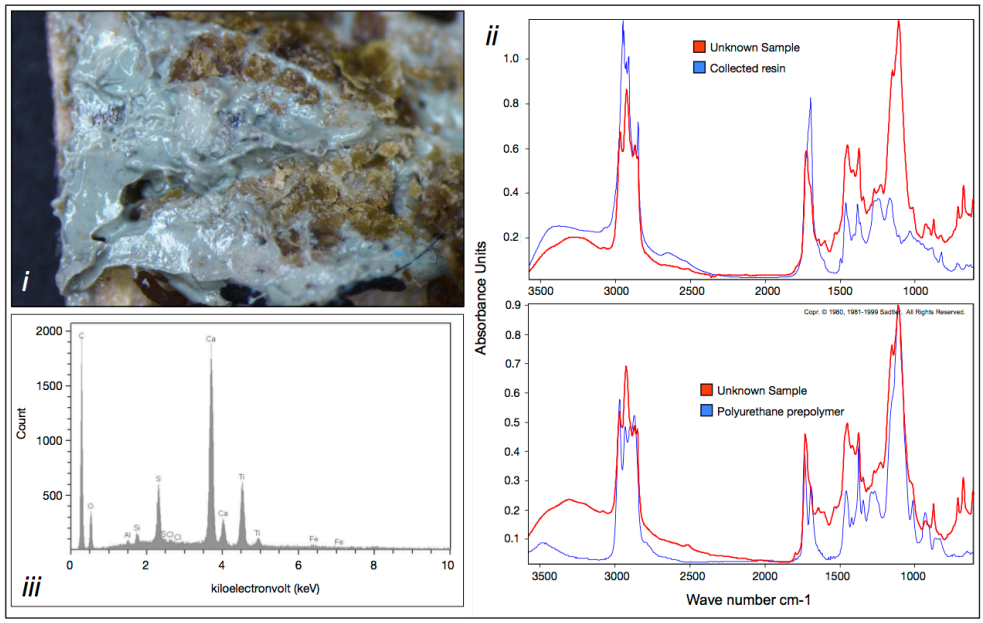

Figure A11. Plate depicting the novel nesting material and the analyses used to determine its structural and chemical composition. (*i*) Non-resin material found in the nest of *Megachile campanulae* in downtown Toronto, Canada. (*ii*) FTIR spectra demonstrating how the composition differs from the *M. campanulae* natural nest resin and has similar characteristics to common polyurethane polymers. (*iii*) Energy dispersive x-ray spectrum reading of the substance collected by *M. campanulae* as a nesting material substitute.

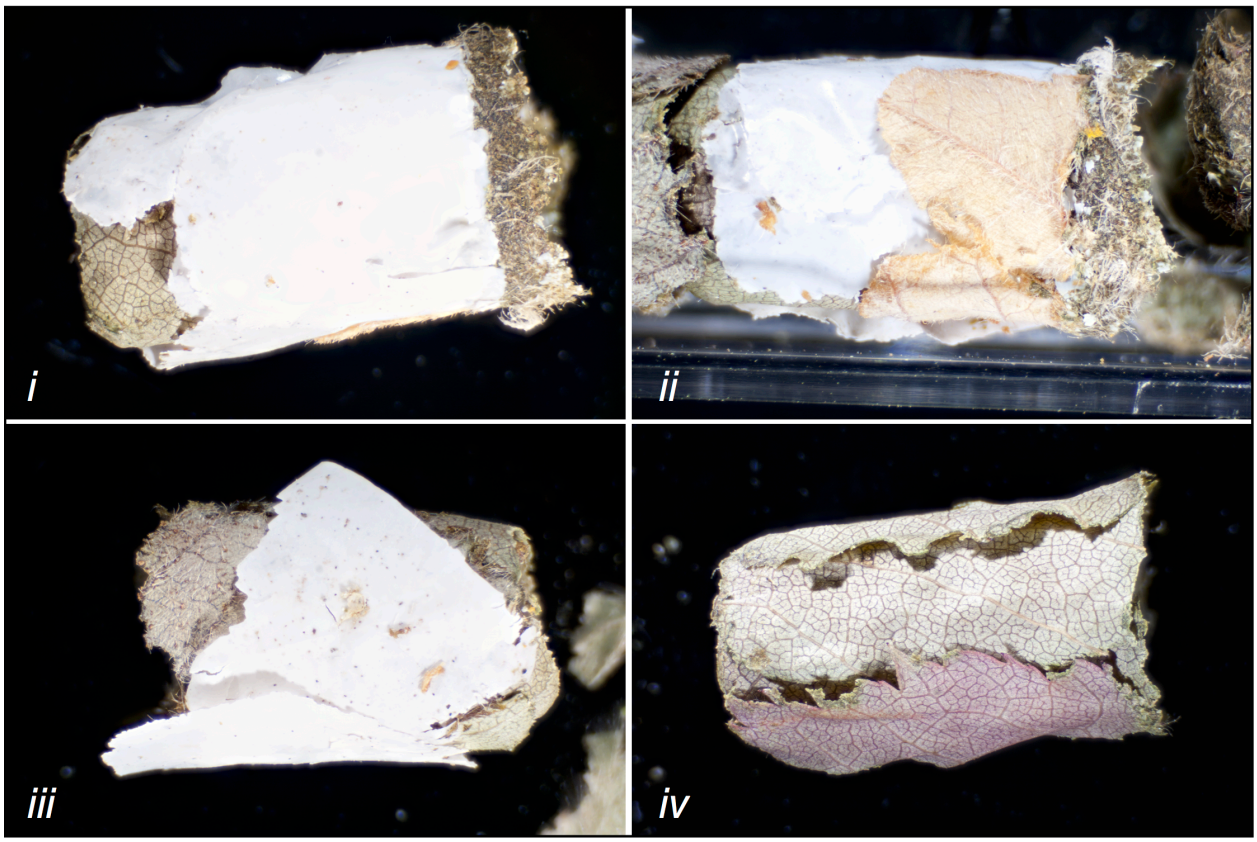

Figure A12. Plate depicting *Megachile rotundata* brood cells made with and without polyethylene plastics. *M. rotundata* brood cell #5 (*i*), #6 (*ii*), #7 (*iii*) are partially constructed using polyethylene plastic bag fragments and one cell comprised of leaves only (*iv*).

Appendix P. RESEARCH ARTICLE: Building height matters: Nesting activity of bees and wasps on vegetated roofs

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1. Abstract

Vegetated, “green” infrastructure, including terraces, balconies, and vegetated roofs and walls are increasingly common in urban landscapes, elevating habitat into novel contexts above ground. Highly mobile species, like bees and wasps, are often seen foraging on green infrastructure, but whether nesting opportunities are facilitated is not known. Cavity-nesting bees and wasps that provision brood in human-made trap nests were monitored over three years on 29 vegetated and nonvegetated roofs in Toronto, Canada. The study identified 27 species nesting on rooftops but found that building height was negatively correlated with the abundance of brood cells provisioned in trap nests, and positively correlated with the number of unfinished nests. A decline in green space area within a 600 m radius around each rooftop resulted in decreasing species richness and abundance. Although the introduced bee, *Megachile rotundata* (Fabricius) occupied more sites than any other bee or wasp (27.6%) and was the most abundant species, amounting to half (48.9%) of all brood reared, native bees were 73% of all bee species reared. The most abundant wasp was the native spider-collecting *Trypoxylon collinum* Smith (11.4%), but the introduced aphid-collecting *Psenulus pallipes* (Panzer) occurred at more sites (24.1%). For the pollination and pest controlling services they provide, bees and wasps should be considered in the design of vegetated roofs. Evidence here suggests that building height and surrounding green space at ground level impact bee and wasp diversity on vegetated roofs. Efforts supporting their populations using trap nests should target low- and mid-rise buildings (<5 building levels).

2. Introduction

Studies investigating local and landscape impacts on insect populations are increasingly carried out in and around cities (Blair 1999; Hostetler & McIntyre, 2001; Cane et al. 2006; Matteson et al. 2008; Sattler et al. 2010; Bates et al. 2012; Banaszak-Cibicka & Żmihorski 2012; Geslin et al. 2013; Braaker et al. 2014). City landscapes are usually more strongly three-dimensional and complex than surrounding natural landscapes (Allen, 1998). In many cases, city buildings create even more complexity than that on cliff faces or other mountainous habitat (Larson et al. 2004). Studying how taxa interact with thiscomplex environment may provide new insight into their ecology and conservation (Dearborn & Kark 2010).

Green infrastructure elevated above ground in threedimensional space (including vegetated roof and walls, gardened terraces, balconies, and garages) increases green space vertically where space at ground is developed, providing new urban habitat opportunities (Pickett et al. 2013). The contribution of vegetated roofs is perhaps the best studied among them, with some suggesting they could aid in the conservation of rare species, or increase connectivity among fragmented habitat patches (reviewed in Williams et al. 2014). However, vegetated roofs like some ground level habitat might act as dispersal platforms for exotic or undesirable species that undermine native biodiversity conservation. It is important to consider habitat conditions in the design of green infrastructure to facilitate - as well as study - both positive and negative novel responses of biodiversity to urban and environmental changes (McIntyre, 2000; Felson & Pickett 2005; Goddard et al. 2010).

Many species in a wide range of taxonomic groups have been identified from surveys on vegetated roofs (e.g. Jones, 2002; Millet, 2004; Kadas 2006; Pearce & Walters, 2012; Madre et al. 2013; MacIvor et al. 2015; reviewed in MacIvor & Ksiazek, 2015); however, adjacent or nearby ground level reference habitat yields higher diversity (Colla et al. 2009; MacIvor & Lundholm, 2011; Tonietto et al. 2011). There is some quantitative data on the reproductive

success of birds (Baumann 2006) but there are little data on whether vegetated roofs can act as a source or sink for species seeking nesting habitat (MacIvor & Ksiazek 2015). Cavity-nesting bees and wasps in particular may benefit from vegetated roofs as nesting habitat, as they regularly use cracks, crevices, nail- and drill holes in human-made infrastructure, and other cavities as nesting habitat in place of natural ones in wood and plant stems (Krombein 1967; Cane et al. 2007; MacIvor et al. 2014). These include those that are accidentally or intentionally added to vegetated roofs and other forms of green infrastructure. Pollination by bees and predation on pest insects by solitary wasps are desirable ecosystem functions carried out by cavity-nesting species that should be encouraged in both natural and human-dominated landscapes (Tscharntke et al. 1998). However, it is not clear which, if any species of cavity-nesting bees and wasps will search for nesting habitat on roofs of buildings, especially when situated dozens of meters above ground.

Nest site locating behaviors of cavity-nesting bees and wasps often involve vertical movement as the insects search for holes in dead wood in trees (Wcislo, 1996). Thus, cavity nesting bees and wasps might have some pre-adapted traits for searching for nest sites at the heights of vegetated roofs. The use of trap nests (Krombein, 1967) can provide such suitable nesting sites and many cavitynesting species readily adopt them (Tscharntke et al. 1998). Trap nests have been used in many ecological and conservation studies (Gathmann et al. 1994; Steffan-Dewenter et al. 2002; Tylianakis et al. 2006; Praz et al. 2008; MacIvor et al. 2014) and they have been shown to reflect overall bee diversity (Westphal et al. 2008). However, few studies have used trap nests to survey cavity-nesting bees and wasps in urban landscapes (Alves-dos-Santos, 2003; Gaston et al. 2005; Loyola & Martins, 2006; Everaars et al. 2011; Pereira-Peixoto et al. 2014; MacIvor & Packer 2015).

In this study I assess the impact of building height, number of buildings, and the proportion of local ground level green space upon the species richness and abundance of bees

and wasps colonizing trap nests. Horizontal landscape isolation from florally diverse habitats has been correlated with reduced observations of wild bees on flowers (Jauker et al. 2009; Garibaldi et al. 2011). Moreover, increasing horizontal distance from floral resources has resulted in fewer offspring provisioned in cavity-nesting bees (Peterson & Roitberg, 2006; Schüepp et al. 2011). In this study, I hypothesized building height, which reflects vertical isolation from ground level habitat opportunities, would result in decreasing colonization of trap nests by bees and wasps. Further, I hypothesized that as the proportion of green space at ground level increases there would be an increase in colonization of trap nests, as studies sampling bees on vegetated roofs have determined ground level green space to be a predictor of greater abundance and diversity (Tonietto et al. 2011; Braaker et al. 2014).

3. Methods

Bees and wasps were sampled from May to October over three years (2011- 2013) using trap nests set up on 29 rooftops (one per roof) each separated by a minimum 250 m throughout the city of Toronto (Figure A11). The roofs were at varying heights from one (approximately 3.3 m from ground level) to nine building levels (approximately 29.7 m) and were classified into three types: (1) intensively planted vegetated roofs with numerous wild flowers, some shrubs and with growing media deeper than 15 cm; (2) extensive *Sedum* - or grass-dominant vegetated roofs having growing media depths of less than 15 cm (Oberndorfer et al. 2007), and (3) non-vegetated conventional roofs having no vegetation and comprising of rock ballast, asphalt, or bituminous roofing shingles (Table A5). Since rooftop sites in this study were located at different distances from one another, a Moran's I test for spatial autocorrelation and a spatial correlogram in SAM v4.0 (Rangel et al. 2010) were used to examine whether trap nest colonizers from more proximal sites were more similar than what would be expected in a random spatial pattern (Legendre, 1993). It was determined that the trap nests on rooftops in this study were not

spatially autocorrelated (I /Imax = 0.075).

Each trap nest was constructed from a 30 cm piece of recyclable PVC pipe of 10 cm diameter with one end fitted with a pipe cap, the other with a faceplate with 30 cardboard tubes inserted, 10 of each of three widths (3.4, 5.5, and 7.6 mm) plugged at the capped end of the pipe (MacIvor et al. 2014). Trap nests were set up facing southeast and attached using zip-ties to fixed features on the roof in April of each year. Trap nests were not visited again until collection in October, and once recovered the cardboard tubes were opened and the contents analyzed. Species richness and abundance (the number of brood cells reared per trap nest) for bees, wasps, and their parasites were determined once removed from the cardboard tubes. Nest loss was also recorded as the proportion of cell series that were initiated, in which pollen or prey and/or nesting material had been provisioned, but no offspring developed, representing an energetic cost for a surviving female or mortality. Either way, this results in no reproductive success despite reproductive effort and was used as a qualitative means of assessing net negative impacts on the local population.

Local and landscape variables for analysis were calculated using both ground-truthing and geospatial software. Local variables included the number of building levels (“height”) at which the trap nest was set up, and roof vegetation categorization (“planting”). Three categories were identified: intensive, extensive, or none. Intensive referred to vegetated roofs having greater than 15 cm of substrate depth and a more diverse planting than extensive vegetated roofs, which are more shallow (< 15 cm) and support less diverse plantings. Geospatial tools in ArcGIS v.10 (ESRI, Toronto, Canada) using city of Toronto municipal spatial reference data shape files (accessed from the York University Map Library) were used to determine landscape variables: building footprints (“footprint”), number of buildings (“build”), and the proportion of green space within buffered regions surrounding the trap nest sites at 150 m (“X150m”) and 600m (“X600m”) radii. These radii are of similar dimension to other studies examining landscape

factors on bee populations (Steffan-Dewenter et al. 2002; Schüepp et al. 2011; Williams & Winfree, 2013). The area within each buffer occupied by building footprint (m^2) was calculated because it is applicable city wide across different land use zones, and the total building density (number of buildings within an area) was counted because it is correlated with an increasing number of managed gardens (Davies et al. 2008). The proportion of green space surrounding each nest site was calculated using land use shape files from the Toronto and Region Conservation Authority by summing "Open Area" (e.g. open meadows and non-residential lawns) and "Parks and Recreation Area" (e.g. urban parks and forests) land use types.

Including all local and landscape variables, step-wise model selection following Akaike information criterion (AIC) (Burnham & Anderson 2004) was used to determine the best model for interpreting trap nest species richness, abundance, the number of lost cell series (those initiated but incomplete), and parasitism rates. These models of best fit were then analyzed using linear models in R Studio statistical program v0.98 (R Core Team, 2014). A canonical correspondence analysis (CCA) in the R Vegan statistical package (Oksanen, 2013) was implemented to explore correlations between the explanatory local and landscape variables and the abundances of bee, wasp, and parasite species at colonized sites.

4. Results

Twenty-seven species in 16 genera of bee and wasp were recorded from 21 of 29 trap nests colonized over the three-year period (eight trap nests were never colonized over the duration of the study) (Table A6). The 11 bee species (including one cleptoparasite) combined were three times more abundant in trap nests on rooftops than wasps despite 16 species of wasps recorded (including 5 parasites) (Table A6). More native bee and wasp species were recorded than introduced ones; however, the most abundant bee was the introduced *Megachile rotundata*. The bee was collected at 27.6% of sites and accounted for 48.9% of all brood reared

in the study. Due to the dominance of *M. rotundata*, the abundance of introduced bee species outnumbered native bee species in trap nests (Table A6). Among wasps, the most abundant species recorded was the native spider-collecting *Trypoxylon collinum* at 11.4% of the total sample, and 20.9% of sites. The introduced aphid-collecting *Psenulus pallipes* occurred at more site (24.1%), but only 6.6% of the total sample (Table A6). Overall, the most species-rich site included 10 species (in eight genera) and was located on an extensive vegetated roof on the third floor of a private home in a dense residential neighborhood. The most densely occupied trap nests were located on an intensive vegetated roof at the York University Campus where 580 individuals were reared over the three years investigated.

AIC model selection yielded top models for abundance ("height" + "footprint" + "X150m" + "X600m" + "planting"), species richness ("height" + "footprint" + "build" + "X600m" + "planting"), parasitism ("planting"), and the number of incomplete cells ("height" + "planting") that were used for analysis. Relative abundance of bees and wasps declined significantly with increasing building height ($t = 3.240$, $p = 0.004$) (Figure A12) and with decreasing proportion of green space surrounding the building within a 600 m radius ($t = 3.035$, $p = 0.006$) (Figure A13). Species richness did not decline with building height ($t = 1.336$, $p = 0.195$). Species richness was however significantly less on vegetated roofs surrounded by declining proportions of ground level green space within 600 m ($t = 2.341$, $p = 0.029$) (Figure A13). Roof planting type (intensive, extensive, none) had no effect on species richness or abundance but parasitism was highest on intensively planted vegetated roofs ($t = 2.086$, $p = 0.05$). The number of incomplete cell series among all species within a trap nest significantly increased with increasing building height ($t = 3.432$, $p = 0.003$) (Figure A14). There was no effect of the amount of green space at ground level within 150 m of the vegetated roof site.

Some variation in the response of bees, wasps, and parasites to local and landscape variables was evident. The first axis in the CCA captured 36.9% of the variation present in the

data, 22.3% was captured in the second axis, and permutation testing (N = 10,000) demonstrated that the CCA model was a good fit (df = 6, F = 1.27, p = 0.05) (Figure A15). The vectors indicated the amount of green space at 150 and 600 m radii was very similar, each accounting for the proportion of green space in the region around the building. The vectors for building height and the rooftop planting type were different from all ground level landscape variables. Three of the exotic species in the study *Megachile rotundata*, *Osmia caerulescens*, *Passaloecus gracilis* did not respond to any of the variables identified in the biplot and were found on vegetated roofs of all plantings, heights, and landscape conditions.

5. Discussion

Although an increasing number of studies examine which local and landscape factors limit nesting activity of bees and wasps in urban green spaces (Loyola & Martins, 2006; McFrederick & LeBuhn, 2006; Schüepp et al. 2011; Pereira- Peixoto et al. 2014), none address the role of vegetated roofs. Here I demonstrate associations between local (building height) and landscape (surrounding green space at ground level) factors that are implicated in the contribution of vegetated roofs to nesting of cavity-nesting bees and wasps.

Our findings indicate that we can accept our first hypothesis that increasing building height results in decreasing numbers of bees and wasps using in trap nests. Further, of the eight rooftops not colonized over the three-year study, six were extensive and two were conventional and not vegetated; all were over three building levels in height. This is an important detail for those involved in vegetated roof policy and application. For example, the city of Toronto has a vegetated roof by-law and construction standard mandating vegetated roofs on certain new buildings, including residential buildings greater than six building levels (City of Toronto, 2014). Simultaneously, the city encourages best practices for providing wildlife habitat on vegetated roofs (Torrance et al. 2013), without any acknowledgment of site conditions such as building

height on the impact wildlife enhancements may have on local biodiversity. Presumably, even installers of vegetated roofs on condominium buildings, some dozens of meters from ground level, are encouraged to include plans for wildlife on these elevated habitats. This study suggests that plans for encouraging cavity-nesting bees and wasps using trap nests on vegetated roofs need to take into account the height of the building; that is, efforts supporting their populations using trap nests should target low- and mid-rise buildings (< 5 building levels). Our second hypothesis that increasing proportions of surrounding ground level green space contributes to an increase in colonization of bees and wasps in trap nests on rooftops was accepted; however, the R^2 values supporting this significant relationship for species richness and abundance were low (Figure A13) and altogether warrants further study. The proportion of green space surrounding surveyed vegetated roofs was also a significant predictor of bee diversity on six roofs in Chicago (Tonietto et al. 2011).

Despite some bees maintaining a level of constancy in flower foraging height (Waddington & Holden, 1979), when no suitable forage is available, bees may search vertically (Osborne et al. 1999) and thus might have an easier time flying down to ground level. Pollen and nectar are light and can be compacted using hairs and appendages adapted for efficient storage capacity during flight (Schmid-Hempel et al. 1985). This adaptation permits bees to not have to nest too close to foraging resources (Zurbuchen et al. 2010). Since the impact of wind on buildings increases with height (Irwin, 2009), bees and wasps might find it increasingly difficult to travel to and from nests that are higher up and choose to colonize lower roofs instead. Foraging between nearby vegetated roofs might also be possible for bees. Braaker et al. (2014) recently showed that bee diversity collected from 40 vegetated roofs was highly dependent on the connectivity of surrounding vegetated roofs in a dense urban environment.

Wasps that carry relatively large prey such as *Isodontia mexicana* (collects katydids) or *Ancistrocerus antelope* (collects caterpillars) would have a more difficult time flying

back up to the nest than would wasps carrying lighter prey such as *Passaloecus cuspidatus* (collects aphids) or *Trypoxylon collinum* and *Trypoxylon frigidum* (collects spiders) (Hastings, 1986; Coelho 2011). Although not analyzed, in trap nests on rooftops, smaller wasps were more abundant than larger wasps. For cavity-nesting wasps, the energy expended carrying a large prey item up from ground level might be too great and this could limit some species in vertically isolated trap nests on vegetated roofs. Further support is evident in the CCA biplot (Figure A15). The large wasps (e.g. *Ancistrocerus antilope*, *Euodynerus foraminatus*, and *Isodontia mexicana*) were found in the quadrant where vectors representing the proportion of green space surrounding the site were also found, presumably because their prey would be more abundant in green spaces containing their host trees and large shrubs (Krombein, 1967; Ercit, 2014) rather than on or near green infrastructure which is dominated by low growing perennials and grasses.

In this study, there was no difference in richness or abundance of bee and wasp species between the different roof vegetation types (intensive, extensive, none) but parasitism rates were highest on intensive vegetated roofs. Schindler et al. (2011) found no effect of vegetation type on insect diversity on extensive vegetated roofs, but did not examine non-vegetated roofs. These findings do not correspond entirely with other recent studies linking intensively planted vegetated roofs to greater diversity and abundance of insects (Madre et al. 2013). Kadas (2006) also noted a greater diversity of bees on “biodiverse” roofs, and Brenneisen (2006) noted collecting twice as many bees on vegetated roofs with “diverse vegetation” compared to *Sedum*-only ones. At ground level, urban green spaces having more diverse plantings can lead to a greater diversity in bees (Gaston et al. 2005; Cane et al. 2006; Matteson & Langellotto, 2010; Lowenstein et al. 2014). Different from the sampling methods used in the aforementioned studies, I deployed trap nests that when analyzed are indicative of the nesting environment of bees and wasps, and not necessarily the foraging environment. Thus, conditions for foraging created by dense or diverse flowering vegetated roof plantings might not correspond to suitable

nesting habitats, and each need to be addressed together when planning for urban wildlife conservation (Colding, 2007; Williams et al. 2014).

Despite many resources for enhancing cavity-nesting bee and wasp nesting opportunities, more research is needed to elucidate the ecology and diversity of species that successfully occupy habitat along rural-to-highly urban gradients. Although not examined here, behavioural flexibility can allow a species to thrive in urban landscapes will also increase capacity to discern between urban adapting and urban avoiding species (Müller et al. 2013). Data-driven ecological research can then help enhancement strategies and 'designed experiments' by urban planners and municipalities that include nesting material elements and nest analogues for bees and wasps in building integrated habitat (MacIvor & Packer, 2015). These actions could buffer against change in urban landscapes having de-stabilizing effects on bee and wasp species assemblages, regional pollination and pest controlling services, as well as other urban ecosystem services (Tzoulas et al. 2007; Andresson et al. 2014). These activities can serve doubly in public outreach and pollinator stewardship initiatives, as trap nests require little maintenance or cost.

6. References

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7. Tables

Table A5. The height in building levels, and planting type of each rooftop surveyed in the study.

	Building Levels							
	1	2	3	4	5	6	7	9
Extensive	1	2	5	4	3			1
Intensive		2	1	1		2	1	
None			4		1	1		
Total	1	4	10	5	4	3	1	1

Table A6. The number of sites colonized and the abundances of each bee, wasp, and parasite species identified from trap nests set up on rooftops in the study.

Group	Family	Genus	Species	Code	Nest choice (mm)	Sites colonized (%)	Relative Abundance	Total Abundance
Bees	Megachilidae	*Megachile*	***rotundata*** Fabricius	M.rot	5.5	0.276	0.489	1058
			campanulae (Roberston)	M.camp	5.5	0.172	0.026	57
			centuncularis (Linneaus)	M.cent	5.5	0.138	0.022	47
			pugnata Say	M.pug	7.6	0.034	0.002	4
		Osmia	***caerulescens*** (Linneaus)	O.cae	3.4, 5.5	0.207	0.120	257
			lignaria Say	O.lig	5.5	0.034	0.003	7
			pumila Cresson	O.pum	3.4	0.103	0.009	20
		Heriades	*carinata* Cresson	Her.car	3.4,5.5	0.172	0.021	46
	Megachilidae	*Coelioxys*	*sayi* Robertson*[1]	C.say	5.5	0.034	0.0005	1
	Colletidae	*Hylaeus*	*affinis/modestus*	Hyl.sp	3.4	0.103	0.015	33
			leptocephalus (Morawitz)	Hyl.lep	3.4	0.034	0.004	9
Wasps	Sphecidae	*Isodonia*	*mexicana* (Saussure)	I.mex	7.6	0.172	0.028	61
	Crabronidae	*Trypoxylon*	*frigidum* Smith	T.fri	3.4, 5.5	0.138	0.016	35
			collinum Smith	T.col	3.4, 5.5	0.209	0.114	248
			lactitarse Saussure	T.lac	7.6	0.034	0.002	5
		Passaloecus	***gracilis*** (Curtis)	Pas.gra	3.4	0.172	0.012	25
		Psenulus	***pallipes*** (Panzer)	Pse.pal	3.4	0.241	0.068	147
	Vespidae	*Ancistrocerus*	***antilope*** (Panzer)	A.ant	7.6	0.069	0.026	57
			gazella (Panzer)	A.gaz	5.5	0.034	0.004	9
		Euodynerus	*foraminatus* (Saussure)	E.for	5.5, 7.6	0.034	0.005	10
		Symmorphus	*canadensis* (Saussure)	S.can	3.4, 5.5	0.034	0.001	3
			cristatus (Saussure)	S.cri	3.4, 5.5	0.069	0.002	4
	Sapygidae	*Sapyga*	*louisi* Krombein *[2]	Sap.lou	3.4	0.069	0.004	9
	Chrysididae	*Caenochrysis*	*doriae* (Gribodo)*[3]	C.dor	3.4, 5.5	0.103	0.004	8
			tridens (Lepeletier)*[4]	C.tri	5.5	0.034	0.001	3
		Perithous	***divinator*** (Rossi)*[5]	P.div	3.4	0.034	0.0005	1
	Chalcididae	*Monodontomerus*	*obscurus* Westwood*[6]	Mon.obs	-	0.034	0.002	4

8. Figures

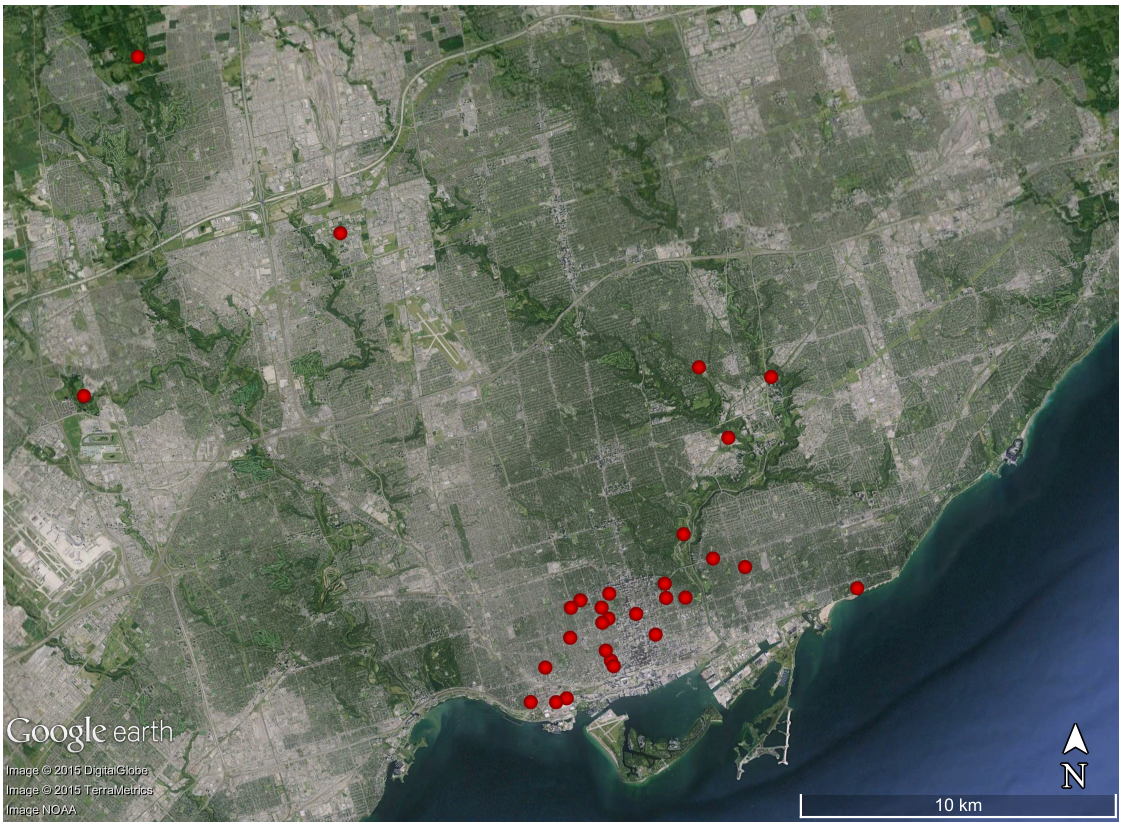

Figure A11. A map of trap nests set up on rooftops in the city of Toronto.

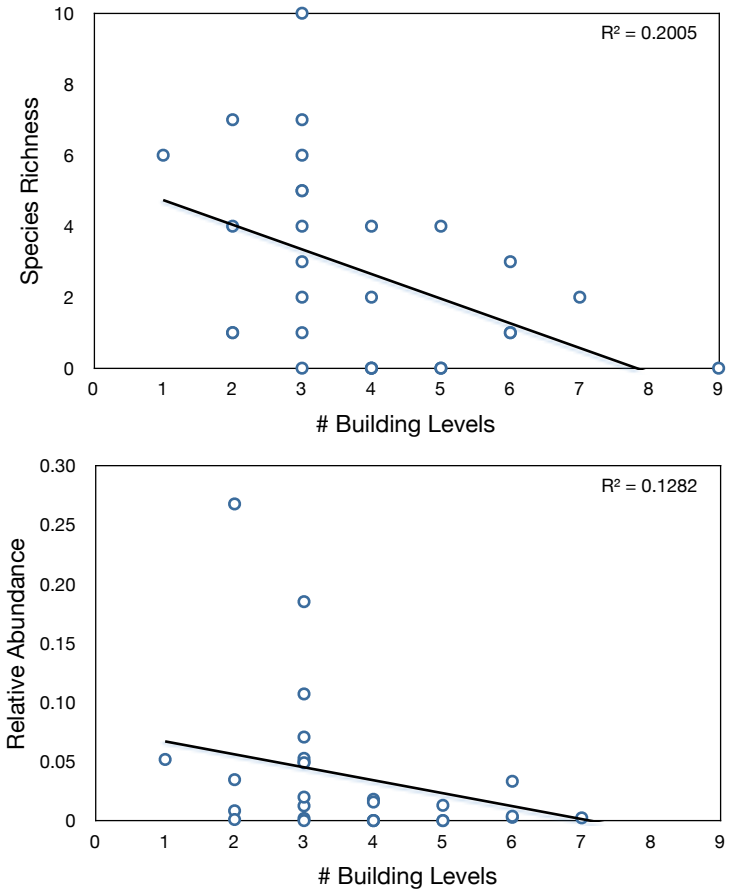

Figure A12. Scatterplots that demonstrate the relationships between increasing building height and (A) species richness (p = 0.195) and (B) declining relative abundance (p = 0.004) in trap nest.

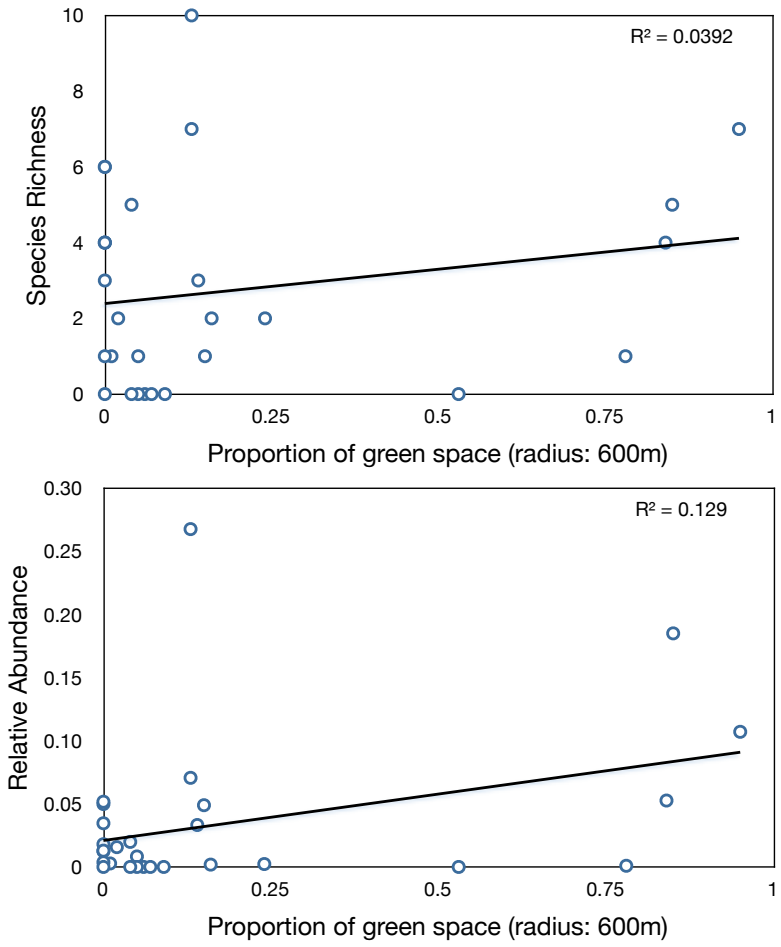

Figure A13. Scatterplots that show that an increasing proportion of green space within a 600 m radius surrounding the rooftop led to increasing (A) species richness and (B) relative abundance ($p = 0.006$).

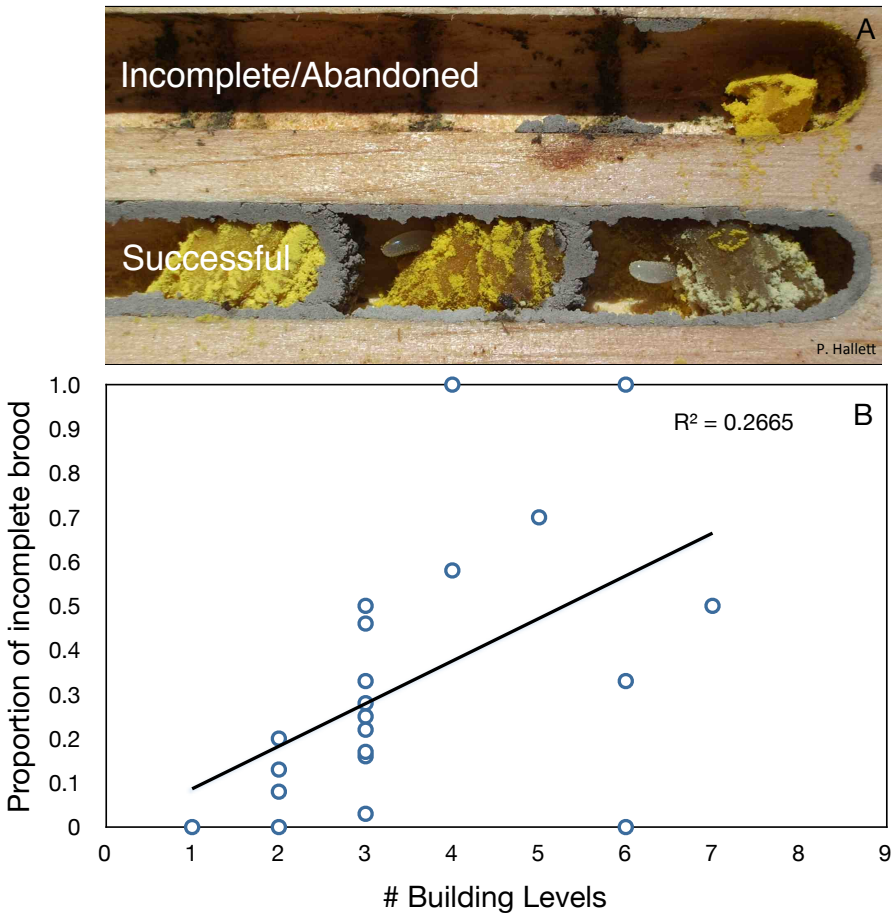

Figure A14. (A) Image of a complete nest and an incomplete nest (or abandoned) of a cavity-nesting bee nest (photo taken by: Peter Hallett) and (B) a scatterplot demonstrating the significant increase ($p = 0.003$) in nest loss by cavity-nesting species with increasing building height.

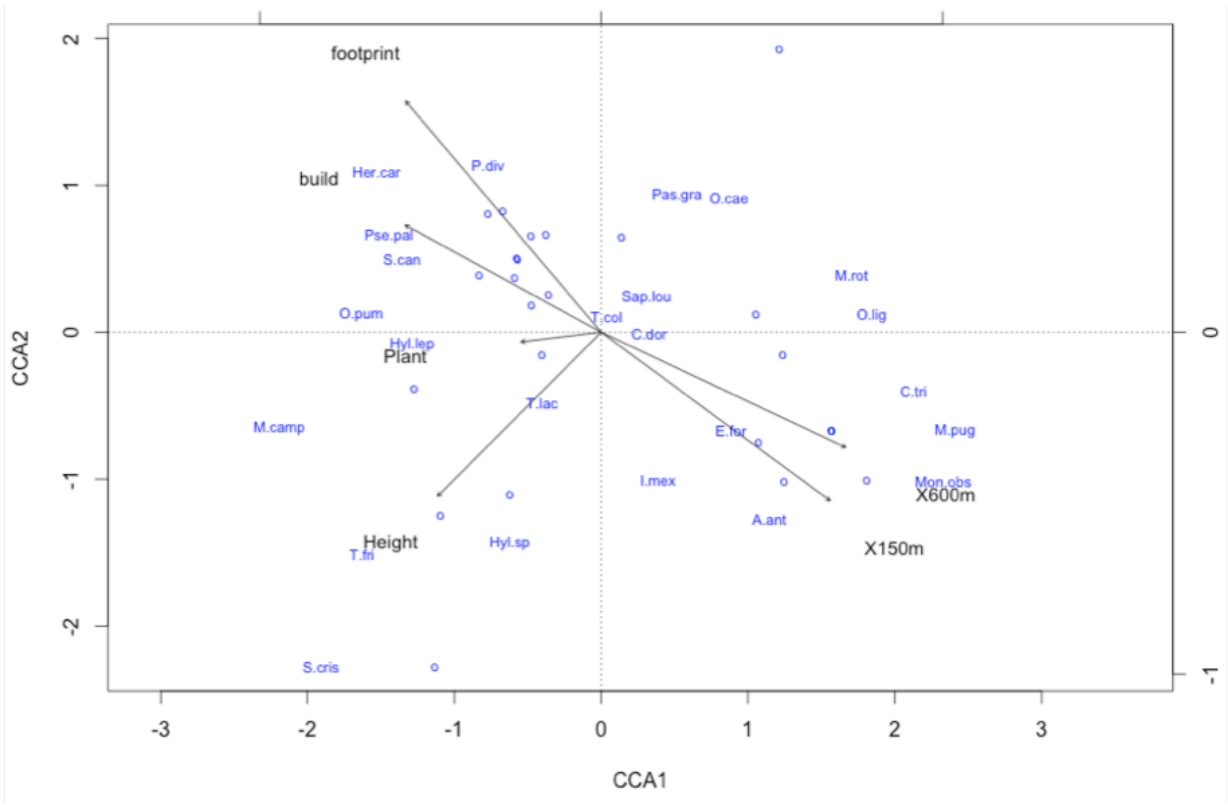

Figure A15. A CCA ordination biplot with local and landscape vectors plotted with bee and wasp species recorded. Vectors are detailed in the methods section and vector acronyms include “footprint” = building footprint within buffer radius, “build” = a count of the number of buildings contained within the buffer radius, “Plant” = the type of roof vegetation (extensive, intensive, none), “Height” = the number of building levels, “X150m” and “X600m” = the proportion of green space within 150 and 600 m buffer radii, respectively. Acronyms for each bee and wasp species are given in Table 2.